THE EFFECTS OF SNOW ON WILDLIFE

ANNOTATED BIBLIOGRAPHY

INTEGRATED WILDLIFE INTENSIVE FORESTRY RESEARCH

Province of British Columbia

A cooperative project between the Ministries of Environment and Forests

THE EFFECTS OF SNOW ON WILDLIFE

Annotated Bibliography

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INTRODUCTION

The objective of this project was to gather and annotate the literature relevant to interactions between snow and animals. Important information is widely dispersed in journals of several disciplines, often as incidental observations. A key to this literature is needed to facilitate current research on the production of winter range for black-tailed deer and Roosevelt elk in areas of deep snow on Vancouver Island. The material collated is also relevant to other wildlife species in other areas of the province.

KEYWORDS

The keywords are a compromise between close delineation and simplicity. Forty-two terms are used. These terms are classified into the following four broad groups:

1. Animal species (16 terms)
2. Snow characteristics (6 terms)
3. Animal response (8 terms)
4. Geographical location (12 terms)

In the keywording found in the text, each broad group is separated by a solidus (/). Examples:

i) (Elk/Snow Depth/Distribution/U.S. Mountains)
ii) (Moose, Bison, Elk, White-tailed Deer//Sinking Depth, Foot Loading/Canadian Mountains)
iii) (Moose/Snow Depth, Snow Hardness/Sinking Depth, Movement/ Arctic-Subarctic)

Note that in example ii), no data on snow characteristics were contained in the paper and consequently keywords for the second broad group are missing. That is indicated by adjacent slashes with no intervening keyword.

Clarification of terms

I Animal Species

Most of the 16 animal species keywords are self-explanatory. The exceptions are as follows:

Many: either refers to a large number of specified species or to a generality applicable to many species.

Other Species: refers to particular species not covered in the keyword list.

II Snow Characteristics

The six snow characteristic keywords refer to those features of snow that are discussed and have been determined as influencing animals. Most of these keywords are self-explanatory (e.g., snow depth, snow hardness, snow duration, and snow density)

Two keywords may be ambiguous:

Climate: indicates that the animals' response to meteorological variables other than snow are also treated. These variables include air temperature, wind speed, and relative humidity.

Slope: refers either to the effects of slope on snow depth or on wildlife distribution.

III Animal Response

The eight animal response keywords refer to how the animals were influenced by snow. That response may be either physical, behavioural, demographical, physiological, or evolutionary. The following keywords may require some clarification:

Distribution: refers to animal spatial patterns relative to snow characteristics, topography, and other animals.

Movement: refers to changes in animal distribution caused by snow.

Energy: refers to the effect of snow on either energy expenditure or energy acquisition.

Food Availability: refers to the effect of snow in altering the amount and distribution of usable food.

Cratering: refers to the specific feeding activity of removing snow with the forefoot or nose.

Foot-Loading: refers to the force exerted per unit area of the foot as the animal stands or moves through the snow.

IV Geographical Location

The twelve geographical location keywords are self-explanatory with the following exception:

General: refers to many areas or to a principle which is applicable to many areas.

Annotated Reference Number

Keyword	1	2	3	4	5	6	7	8	9	10	11	12
Many										X		
Black-tailed Deer												
Sitka Deer												
Mule Deer	X							X				
White-tailed Deer					X							
Moose							X					
Elk			X	X								
Bison												
Caribou/Reindeer		X				X						
Other Ungulates									X			
Wolves												
Humans												X
Other Species											X	
Bighorn Sheep												
Muskoxen												
Mountain Goats												
Snow Depth	X	X	X	X	X	X	X	X	X	X		X
Snow Hardness					X	X		X	X		X	X
Snow Duration							X					
Snow Density										X		
Climate												
Slope												
Distribution		X	X	X				X	X	X		
Movement					X					X		
Sinking Depth										X	X	
Mortality							X					
Energy										X		X
Food Availability	X	X				X			X	X		
Cratering						X						
Foot Loading												
U.S. Mountains	X		X	X								
U.S. West Coast												
Eastern U.S.					X							
Canada Mountains								X				
Canada West Coast												
Eastern Canada						X						
Arctic-Subartic							X					
Boreal Canada												
Antarctic												
Europe												
General										X		X
USSR		X									X	
	1	2	3	4	5	6	7	8	9	10	11	12

Keyword

	Annotated Reference Number											
	13	14	15	16	17	18	19	20	21	22	23	24
Many												
Black-tailed Deer												
Sitka Deer												
Mule Deer						X						
White-tailed Deer				X	X			X	X			
Moose		X	X									X
Elk						X	X					
Bison												
Caribou/Reindeer	X											
Other Ungulates												
Wolves												
Humans												
Other Species												
Bighorn Sheep						X						
Muskoxen												
Mountain Goats												
Snow Depth		X	X	X	X	X	X	X	X		X	X
Snow Hardness	X		X					X				X
Snow Duration												X
Snow Density												
Climate												
Slope												
Distribution					X		X		X		X	X
Movement			X				X	X			X	
Sinking Depth			X					X				
Mortality		X						X				
Energy												
Food Availability	X			X		X		X			X	X
Cratering												
Foot Loading												
U.S. Mountains							X					
U.S. West Coast												
Eastern U.S.				X	X							
Canada Mountains						X						
Canada West Coast												
Eastern Canada								X	X		X	
Arctic-Subartic	X	X	X									
Boreal Canada												X
Antarctic												
Europe												
General												
USSR												
	13	14	15	16	17	18	19	20	21	22	23	24

Keyword

	Annotated Reference Number											
	25	26	27	28	29	30	31	32	33	34	35	36
Many			X									
Black-tailed Deer	X										X	X
Sitka Deer												
Mule Deer	X					X			X			
White-tailed Deer					X		X			X		
Moose	X											
Elk				X								
Bison												
Caribou/Reindeer		X										
Other Ungulates												
Wolves												
Humans								X				
Other Species	X								X			
Bighorn Sheep												
Muskoxen												
Mountain Goats												
Snow Depth	X		X	X	X	X			X	X	X	X
Snow Hardness		X	X	X								
Snow Duration			X					X				
Snow Density												
Climate												
Slope												
Distribution			X	X	X	X	X			X	X	X
Movement			X	X							X	X
Sinking Depth		X	X									
Mortality	X		X									
Energy								X				
Food Availability			X	X					X		X	X
Cratering												
Foot Loading												
U.S. Mountains				X		X			X			
U.S. West Coast												
Eastern U.S.					X		X			X		
Canada Mountains												
Canada West Coast											X	X
Eastern Canada												
Arctic-Subartic	X											
Boreal Canada	X											
Antarctic												
Europe												
General								X				
USSR		X	X									
	25	26	27	28	29	30	31	32	33	34	35	36

Keyword	Annotated Reference Number											
	37	38	39	40	41	42	43	44	45	46	47	48
Many		X										
Black-tailed Deer	X							X				
Sitka Deer												
Mule Deer											X	
White-tailed Deer					X	X				X		X
Moose												
Elk	X						X					
Bison												
Caribou/Reindeer				X								
Other Ungulates												
Wolves												
Humans			X									
Other Species									X			
Bighorn Sheep												
Muskoxen												
Mountain Goats												
Snow Depth	X		X	X	X		X	X	X	X	X	X
Snow Hardness	X			X		X						
Snow Duration												
Snow Density												
Climate												
Slope												
Distribution				X			X					X
Movement					X					X		
Sinking Depth	X		X			X			X			
Mortality												
Energy	X		X									
Food Availability	X							X			X	X
Cratering				X								
Foot Loading												
U.S. Mountains							X				X	
U.S. West Coast								X				
Eastern U.S.						X				X		
Canada Mountains												
Canada West Coast												
Eastern Canada					X							X
Arctic-Subartic				X								
Boreal Canada												
Antarctic												
Europe												
General	X	X	X						X			
USSR												
	37	38	39	40	41	42	43	44	45	46	47	48

CROSS-REFERENCE TABLE (continued)

Annotated Reference Number

Keyword	49	50	51	52	53	54	55	56	57	58	59	60
Many												
Black-tailed Deer			X									
Sitka Deer												
Mule Deer												
White-tailed Deer	X			X	X	X	X					
Moose				X	X	X	X					
Elk		X				X	X			X		
Bison						X	X					
Caribou/Reindeer								x	x		x	
Other Ungulates												
Wolves												
Humans												
Other Species												
Bighorn Sheep												
Muskoxen												x
Mountain Goats												
Snow Depth	X		X		X			X	X	X	X	X
Snow Hardness			X	X	X			X	X		X	
Snow Duration		X										
Snow Density					X							
Climate												
Slope												
Distribution		X	X		X			X		X	X	
Movement												
Sinking Depth				X	X	X	X					
Mortality												X
Energy	X											
Food Availability			X					X	X		X	
Cratering												
Foot Loading						X	X					
U.S. Mountains		X								X		X
U.S. West Coast												
Eastern U.S.	X			X	X							
Canada Mountains						X	X					
Canada West Coast			X									
Eastern Canada												
Arctic-Subartic								X			X	
Boreal Canada												
Antarctic									X			
Europe												
General												
USSR												
	49	50	51	52	53	54	55	56	57	58	59	60

Keyword

	Annotated Reference Number											
	61	62	63	64	65	66	67	68	69	70	71	72
Many												
Black-tailed Deer										X		
Sitka Deer												
Mule Deer	X	X							X		X	X
White-tailed Deer				X	X							
Moose												
Elk						X						
Bison							X	X				
Caribou/Reindeer												
Other Ungulates												
Wolves									X			
Humans			X									
Other Species												
Bighorn Sheep												
Muskoxen												
Mountain Goats												
Snow Depth	X	X	X			X	X	X	X	X	X	X
Snow Hardness									X			
Snow Duration		X										
Snow Density												
Climate		X										X
Slope												
Distribution		X				X	X	X		X		
Movement		X										
Sinking Depth									X			
Mortality	X						X		X			
Energy			X	X	X							X
Food Availability							X	X		X	X	X
Cratering												
Foot Loading												
U.S. Mountains	X	X					X	X				
U.S. West Coast										X		
Eastern U.S.									X		X	
Canada Mountains						X						
Canada West Coast												
Eastern Canada												
Arctic-Subartic												
Boreal Canada												
Antarctic												
Europe												
General			X									X
USSR												
	61	62	63	64	65	66	67	68	69	70	71	72

CROSS-REFERENCE TABLE (continued)

Keyword

	Annotated Reference Number											
	73	74	75	76	77	78	79	80	81	82	83	84
Many		X	X									
Black-tailed Deer												
Sitka Deer												
Mule Deer												
White-tailed Deer				X	X	X						
Moose	X						X	X	X	X		
Elk												X
Bison												
Caribou/Reindeer												
Other Ungulates												
Wolves									X	X		
Humans												
Other Species												
Bighorn Sheep											X	
Muskoxen												
Mountain Goats											X	
Snow Depth	X		X	X	X	X	X	X	X	X	X	X
Snow Hardness			X	X		X	X		X			
Snow Duration												
Snow Density							X					
Climate					X							
Slope												
Distribution			X	X	X		X	X		X		X
Movement		X	X									
Sinking Depth			X	X					X	X		
Mortality			X						X	X		
Energy											X	
Food Availability	X		X	X								
Cratering												
Foot Loading												
U.S. Mountains												X
U.S. West Coast												
Eastern U.S.	X			X	X		X	X	X	X		
Canada Mountains											X	
Canada West Coast												
Eastern Canada						X						
Arctic-Subartic												
Boreal Canada												
Antarctic												
Europe												
General		X										
USSR			X									
	73	74	75	76	77	78	79	80	81	82	83	84

CROSS-REFERENCE TABLE (continued)

Keyword

	Annotated Reference Number											
	85	86	87	88	89	90	91	92	93	94	95	96
Many					X							
Black-tailed Deer												
Sitka Deer												
Mule Deer												
White-tailed Deer												X
Moose			X								X	X
Elk												
Bison												
Caribou/Reindeer				X		X		X	X	X		X
Other Ungulates												X
Wolves												X
Humans												
Other Species	X	X					X					
Bighorn Sheep												
Muskoxen												
Mountain Goats												
Snow Depth			X	X	X	X	X	X		X	X	X
Snow Hardness				X	X	X	X	X		X		
Snow Duration												
Snow Density						X						
Climate	X							X				
Slope												
Distribution			X	X	X	X	X			X	X	X
Movement				X		X						
Sinking Depth	X	X		X								
Mortality					X							
Energy					X							
Food Availability												X
Cratering				X		X		X				X
Foot Loading												X
U.S. Mountains												
U.S. West Coast												
Eastern U.S.			X									
Canada Mountains												
Canada West Coast												
Eastern Canada												
Arctic-Subartic				X		X	X					
Boreal Canada												
Antarctic												
Europe										X	X	X
General					X			X	X			
USSR	X	X										X
	85	86	87	88	89	90	91	92	93	94	95	96

Keyword

	Annotated Reference Number											
	97	98	99	100	101	102	103	104	105	106	107	108
Many												
Black-tailed Deer		X										
Sitka Deer		X										
Mule Deer			X			X						
White-tailed Deer				X	X		X				X	X
Moose												
Elk												
Bison												
Caribou/Reindeer								X	X			
Other Ungulates												
Wolves												
Humans	X											
Other Species												
Bighorn Sheep												
Muskoxen												
Mountain Goats												
Snow Depth	X	X	X	X	X	X	X				X	X
Snow Hardness												
Snow Duration											X	
Snow Density			X									
Climate												X
Slope												
Distribution		X			X	X						X
Movement												
Sinking Depth												
Mortality											X	
Energy	X			X								
Food Availability		X	X				X					X
Cratering			X					X	X			
Foot Loading			X							X		
U.S. Mountains			X			X	X					
U.S. West Coast		X										
Eastern U.S.				X	X						X	X
Canada Mountains												
Canada West Coast												
Eastern Canada												
Arctic-Subartic												
Boreal Canada										X		
Antarctic												
Europe												
General												
USSR								X	X			
	97	98	99	100	101	102	103	104	105	106	107	108

CROSS-REFERENCE TABLE (continued)

Keyword	Annotated Reference Number											
	109	110	111	112	113	114	115	116	117	118	119	120
Many												
Black-tailed Deer												
Sitka Deer												
Mule Deer												
White-tailed Deer		X			X			X	X	X		
Moose	X	X						X	X	X		
Elk				X			X			X		
Bison										X		
Caribou/Reindeer			X			X						
Other Ungulates												
Wolves												
Humans												
Other Species												X
Bighorn Sheep												
Muskoxen												
Mountain Goats												
Snow Depth	X	X	X	X	X	X	X	X	X			
Snow Hardness			X			X	X					
Snow Duration												
Snow Density												
Climate												
Slope												
Distribution	X	X	X	X	X	X	X	X	X			
Movement				X			X	X				
Sinking Depth									X	X		X
Mortality												
Energy												
Food Availability												
Cratering			X				X					
Foot Loading												
U.S. Mountains		X					X					
U.S. West Coast												
Eastern U.S.					X					X		
Canada Mountains												
Canada West Coast												
Eastern Canada								X	X			
Arctic-Subartic						X						
Boreal Canada	X											
Antarctic				X								
Europe			X									
General												
USSR												X
	109	110	111	112	113	114	115	116	117	118	119	120

CROSS-REFERENCE TABLE (continued)

Keyword	Annotated Reference Number									
	121	122	123	124	125	126	127	128	129	130
Many										
Black-tailed Deer										X
Sitka Deer										
Mule Deer							X			
White-tailed Deer				X	X	X			X	
Moose										
Elk										
Bison										
Caribou/Reindeer	X	X								
Other Ungulates										
Wolves										
Humans										
Other Species										
Bighorn Sheep										
Muskoxen										
Mountain Goats										
Snow Depth	X	X		X	X	X	X		X	X
Snow Hardness	X				X	X				
Snow Duration										
Snow Density										
Climate										
Slope									X	
Distribution		X		X			X			X
Movement	X									
Sinking Depth					X					
Mortality					X	X	X			
Energy										
Food Availability		X		X					X	
Cratering	X									
Foot Loading										
U.S. Mountains							X			
U.S. West Coast										
Eastern U.S.				X	X	X			X	
Canada Mountains										
Canada West Coast										X
Eastern Canada										
Arctic-Subartic	X									
Boreal Canada										
Antarctic										
Europe										
General										
USSR		X								
	121	122	123	124	125	126	127	128	129	130

BIBLIOGRAPHY

1 Anonymous. 1969. Forestry research highlights. USDA For. Serv., Rocky Mountain For. and Range Expt. Sta., 42 pp.

(Mule Deer/Snow Depth/Food Availability/U.S. Mountains)

Page 14 discusses snow as an obstacle to forage availability for mule deer in Colorado: "... tame deer used [forbs and grasses] in proportion to their availability, which was determined by snow depth. Browse use was high only when there was continuous deep snow, and highest when the snow was deep and crusted."

2 Avranchik, M.N. 1939. Zimnee pitanie olenei na Yamal 'skom severe (The winter feeding of reindeer in the Yamal north). Leningrad: Scientific Research Institute of Polar Agriculture, Reindeer Husbandry Ser. No. 4.

(Reindeer/Snow Depth/Distribution, Food Availability/ USSR)

Reindeer travel and feed in shallow snow. In hillocky bogs, they dig for lichens only on the hillocks where the snow is more shallow.

Not seen - cited in LaPierre and Lent (1977).

3 Baglien, J.W., and D.E. Biggens. 1976. A plan for elk management by habitat management. Proc. Elk-Logging Roads Symp., Univ. of Idaho, pages 81-84.

(Elk/Snow Depth/Distribution/U.S. Mountains)

Severe conditions (90-120 cm of crusted snow) are accompanied by greater elk use of timbered areas.

4 Beall, R.C. 1974. Winter habitat selection and use by a western Montana elk herd. Ph.D. dissertation, Univ. of Montana, Missoula. 197 pp.

(Elk/Snow Depth/Distribution/U.S. Mountains)

A general discussion of winter habitat selection and use by elk. The discussion of movements (radio-telemetry) within areas of different snow depth is of some relevance (pp.62-83). "When the snow depth approached 18 inches [46 cm], elk began moving lower to areas of lesser snow depth. This occurred at shallower snow depths when a heavy crust was present. ... This does not imply that elk are unable to travel in snow depths greater than 18 inches, for elk were observed to travel through soft snow depths in excess of three feet. However, the energy expenditure apparently is such, particularly with a crust, that the animals are

reluctant to travel through deep snow" (p.80).

5 Behrend, D.F. 1966. Correlation of white-tailed deer activity, distribution and behavior with climatic and other environmental factors. New York Dept. Conserv., Job Compl. Rept. P-R Project W-105-R.7. 123 pp. Unpubl.

(White-tailed deer/Snow Depth, Snow Hardness/Movement/ Eastern U.S.)

"The hazard which deer encounter from accumulated snow depends upon its depth and supporting quality; the combined effects govern their freedom of movement and habitat use in the yarding area".

Not seen - quoted from Ozoga (1968).

6 Bergerud, A.T., and M.J. Nolan. 1970. Food habits of hand-reared caribou Rangifer tarandus L. in Newfoundland. Oikos 21: 348-350.

(Caribou/Snow Depth, Snow Hardness/Food Availability, Cratering/Eastern Canada)

The food habits of hand-reared caribou were examined in a 0.5 ha pen in Newfoundland. In January and February, when snow depths exceeded 25 cm, caribou failed to crater for terrestrial lichens. The authors suspected that caribou could scent lichens beneath the snow. Caches of lichens were made under snowpacks of varying depths and densities. Caribou had no difficulty in locating lichens under 18 cm of porous snow, but failed to crater for caches under snow 25 cm deep. However, when air vents were made with a small stick, the lichens were easily discovered. It is suggested that stems protruding through the snowpack provide natural air vents.

7 Bishop, R.H., and R.A. Rausch. 1974. Moose population fluctuations in Alaska, 1950-1972. Naturaliste Can. 101: 559-593.

(Moose/Snow Depth, Snow Duration/Mortality/Arctic-Subarctic)

Snow depth and duration was implicated in winter survival of moose in Alaska. Official snow depth records were graphed and the area under the curve taken as an index of snow conditions. This index was clearly related to moose winter mortality. March and April were the critical months during which deep snow caused high mortality.

8 Bouckhout, L.W. 1972. The behaviour of mule deer (Odocoileus hemionus hemionus Rafinesque) in winter in relation to the social and physical environment. M.Sc. thesis, Univ. of Calgary. 124 pp.

(Mule Deer/Snow Depth, Snow Hardness/Distribution/ Canadian Mountains)

After a heavy snowfall in early January, deer moved out of Watertown townsite and onto conifer slopes. Crusts form more slowly under conifer canopies and less snow collects. In late January, wind had bared portions of open areas while snow remained deep in the forest. Deer then moved out into the open to feed. One old doe was particularly adept at leading her group to areas of most favourable conditions.

9 Bruns, E.H. 1969. A preliminary study of behavioural adaptations of wintering pronghorn antelopes. M.Sc. thesis, Univ. of Calgary, Calgary.

(Other Ungulates/Snow Depth, Snow Hardness/Food Availability, Distribution/)

It is suggested that pronghorns are not "chionophobes" as reported by Pruitt (1960). Pronghorns spent 6.7 - 11.5% of their feeding time pawing. Considerable pawing was observed even when food was available above the snow. It is suggested that the snow mantle improved forage quality by protection from dessication. Pronghorns selected microhabitats with snow that was 76% as deep, 13% as hard, and 66% as dense as the average.

10 Bunnell, F.L. 1978. Snow, trees, and ungulates. Rept. to British Columbia Fish and Wildlife Branch CARP. 72 pp.

(Many Species/Snow Depth, Snow Density/Energy, Sinking Depth, Food Availability, Movement, Distribution/ General)

A literature review of the effects of snow, as influenced by topography and forests, on ungulate habitat use and locomotion. Parts I, II and III deal with factors affecting snow depth, density and distribution. Part IV reviews foot-loading and chest height as adaptations; develops a generalized model for sinking depth and locomotion restriction based on snow depth and density; and reviews the interaction of several ungulate species with trees and snow.

11 Burdukov, G.N., and V.M. Kozlov. 1979. Experiment in measuring the specific load of animals on snow. Soviet J. Ecology 10: 87-89.

(Other Species/Snow Hardness/Sinking Depth/USSR)

Notes that treating foot loading as body weight divided by foot area ignores the fact that weight is borne on various numbers of extremities during various gaits. Foot loading also depends upon speed of movement and degree of acceleration. A spring-activated dynometer was punched into the snow to track depth to determine actual foot-loading. Static loads for marten varied from 20-28 g cm^{-2} whereas dynamic loads were 36-40 g cm^{-2}. Wolverine have lower static loadings than lynx but bound through the snow and therefore sink as deep as lynx. Dynamic loadings are listed for several medium-sized boreal mammals. The fringe on the toes of black grouse allows them the surface area needed to spring into the air from snow surfaces.

12 Christensen, E.H., and P. Hogberg. 1951. Physiology of skiing. Arbeitsphysiologie 14: 292-303.

(Humans/Snow Depth, Snow Hardness/Energy/General)

Subjects included males and females from 14 to 35+ years; all experienced skiers by North American standards including some of Sweden's best at the time of experiment. The study contradicts early statements of Liljestrand and Stenstrom (1920) that walking and running were more 'economical' means of transportation than skiing, even on relatively loose snow. Twelve tables and six figures of data are presented. Major points include: 1) among individuals with high capacity for Oxygen uptake, uptake increased linearly with increasing speed from 4 to 15 km h^{-1} (asymptotic among individuals with lower capacity), 2) energy output probably did not increase at the same rates but was delivered by anaerobic processes, 3) in competition, heart rates 10 sec after finish were: >240 (14-16 year old males, 5 km); 250-270 (15-17 year old females, 5 km); 214 (adult females, 18 km); >200 (adult males, 18 km), 4) proteinuria usually occurred. 5) skiing is more efficient than walking or snowshoeing, even in loose snow going uphill; gradient 1:8, 6) nevertheless, energy output during skiing is high, 7) Walking on soft snow at speeds of 60-66 m sec^{-1} while carrying a 20 kg load entails energy expenditures of 15.2-20.2 kcal min^{-1}. On hard snow, at speeds of 100-152 m min^{-1}, the cost varied from 8.4 - 16.2 kcal min^{-1}. No data on sinking depth are given.

13 Claggett, G.P. 1978. Surveying snow in arctic Alaska to determine its effects on reindeer herding. Proc. Western Snow Conf. 46: 63-68.

(Reindeer/Snow Hardness/Food Availability/Arctic-Subarctic)

A preliminary study of snow characteristics on reindeer range in Alaska. Ramsonnde determinations were made at various aspects. Five kg of hardness was the minimum that would support a man's weight without snowshoes. Crusts of 9-10 kg resistance restricted foraging by reindeer. Total area under the RAM curve may be more significant since a thin, hard layer may not pose as great a problem as a thick, softer one.

14 Coady, J.W. 1973. Moose research report. Fed. Aid. Wildl. Rest. Proj. Seg. Rep., Alaska Fish and Game, Juneau.

(Moose/Snow Depth/Mortality/Arctic-Subarctic)

An examination of winter severity trends by plotting weather records of snow depth vs month and measuring the area under the curve. Substantial moose mortality occurred when snow depths > 90 cm were experienced for several months.

Not seen - cited in Coady (1974).

15 Coady, J.W. 1974. Influence of snow on behaviour of moose. Naturaliste Can. 101: 417-436.

(Moose/Snow Depth, Snow Hardness/Sinking Depth, Movement/Arctic-Subarctic)

Prefaced with a useful review of wildlifers' approach to snow measurement. Snow depths up to 40 cm caused little hindrance to moose. Depths of 60-70 cm, or 2/3 of chest height, only slightly restricted movement. Depths greater than 70 cm were associated with definite restriction in movement whereas depths > 90 cm were greatly restricting. Foot loads of moose varied with age and season. Calves had lower foot loadings. The Ramsonnde penetrometer was used to determine integrated hardness to depth of the track. Preliminary results appear equivocal. An extensive review is provided of the effect of snow on moose movements. Moose movement, ram hardness, and snow depth were compared for an area near Fairbanks.

16 Coblentz, B.E. 1970. Food habits of George Reserve deer. J. Wildl. Manage. 34: 535-540.

(White-tailed Deer/Snow Depth/Food Availability/Eastern U.S.)

A strong correlation was found in the percentage of browse used by deer and snow depth. With no snow, browse use averaged 37% of total food intake whereas snow depths of 3 inches or more were accompanied by 100% browse intake.

17 Cook, D.B., and W.J. Hamilton, Jr. 1942. Winter habits of white-tailed deer in Central New York. J. Wildl. Manage. 6: 287-291.

(White-tailed Deer/Snow Depth/Distribution/Eastern U.S.)

The Adirondacks are characterized by a cold climate and deep snow. Deer therefore concentrate in evergreen swamps when the snow becomes deep enough to make travel difficult. In central New York, where the climate is milder and snow less deep, deer concentrate on steep south and southeast slopes regardless of cover type. Such slopes are sheltered from the prevailing west wind and receive much sunlight. Snow is substantially less deep on such slopes. Wind and snow are the two factors which most affect the choice of deer winter range.

18 Cowan, I.McT. 1947. Range competition between mule deer, bighorn sheep, and elk in Jasper Park, Alberta. Trans. N. Amer. Wildl. Conf. 12: 223-227.

(Mule Deer, Elk, Bighorn Sheep/Snow Depth/Food Availability/Canadian Mountains)

A study of winter food habits of mule deer, elk and bighorn sheep by direct observation during a period of little or no snow. It was expected that 6 inches of snow would alter the nature of the diet consumed by deer and that deep snow would cause elk to switch from grass to browse.

19 Craighead, J.J., F.C. Craighead Jr., R.L. Ruff, and B.W. O'Gara. 1973. Home ranges and activity patterns of nonmigratory elk of the Madison Drainage herd as determined by biotelemetry. Wildl. Monogr. 33: 1-50.

(Elk/Snow Depth/Distribution, Movement/U.S. Mountains)

Elk in Yellowstone wintered in thermal areas where snow depths were minimal. Winter movements were so restricted that no animal was observed to move > 1 airline mile in 24 hr. Elk moved into surrounding lodgepole pine forest to feed but never moved through 4-5 ft snow cover for more than 300 yards.

20 Crete, M. 1976. Estimation of winter mortality of deer in Quebec. Can. Field-Natur. 90(4): 397-403.

(White-tailed Deer/Snow Depth, Snow Hardness/Food Availability, Sinking Depth, Mortality, Movement/Eastern Canada)

Every two weeks, measurements were made of snow depth,

snow hardness (using Verme's 1968 apparatus), air temperature, deer-track density, sinking depth of deer, and average diameter of grazed twigs. Dropping the compaction guage from 5 cm gave a correlation to sinking depth of 0.78. Diameter of browsed twigs was related to sinking depth, to progression of the winter, to snow depth, and to temperature. The diameter of browsed twigs was successful in predicting winter mortality.

21 Cumming, H.G., and F.A. Walden. 1970. The white-tailed deer in Ontario. Ontario Dept. Lands and Forests. 25 pp.

(White-tailed Deer/Snow Depth/Distribution/Eastern Canada)

Snow depths of 20 inches caused white-tailed deer to concentrate.

Not seen - cited in Jones (1975).

22 Davydov, A.F. 1963. On the regime of muscle activity in reindeer when obtaining food from under the snow. Physiol. Invest. Adaptation in Animals 6: 35-40 (in Russian).

(Keywords to come)

Not seen

23 Des Moules, P. 1964. The influence of snow on the behaviour of moose. Trans. Northeast Wildl. Conf. 21: 1-17 and Pages 51-68 in: Traveux en Cours en 1963. Rapport No. 3. Service de la fauna du Quebec, Ministre du Tourisme.

(Moose/Snow Depth/Food Availability, Distribution, Movement/Eastern Canada)

A study of the effect of snow on moose in Laurentides Provincial Park, Quebec. Cross-sections of typical quamaniq depressions are shown for balsam fir and white birch. Snow-depths under various canopy types are presented. In early winter, moose bedded in deep snow areas (cut-over hardwoods). As snow depths increased, beds were found increasingly often under more closed canopies. At snow depths of 30-34 inches, moose shifted activity from cut-over areas to small- or medium-sized openings. They rarely entered areas with more than 42-48 inches of snow. The deeper the snow, the more restricted the moose became to quamaniqs. This resulted in a shift to coniferous browse. As snow depth increased, moose broke up into smaller groups.

24 Eastman, D.S. 1978. Habitat selection and use in winter by moose in sub-boreal forests of north-central British Columbia, and relationships to forestry. Ph.D. thesis, Univ. of British Columbia, Vancouver, B.C. 554 pp.

(Moose/Snow Depth, Snow Hardness, Snow Duration/ Distribution, Food Availability/Boreal Canada)

Chapter 9 presents an analysis of the effects of forests on winter climate, largely snow (see Forest-Snow annotated bibliography); pages 370-378 discuss the relationship between snow depth and forest canopy. The effect of snow on moose migration and habitat use is discussed. Moose shifted to forested habitat as snow depths approached critical levels. Snow density was usually of little importance although it may be of greater importance in low snowfall areas. Quamaniqs were extensively used by moose. Moose use of an apparently uniform forest type was non-random; they selected microsites.

25 Edwards, R.Y. 1956. Snow depths and ungulate abundance in the mountains of western Canada. J. Wildl. Manage. 20: 159-168.

(Mule Deer, Black-tailed Deer, Moose, Others/Snow Depth/ Mortality/Boreal Canada, Arctic-Subarctic)

Ungulate population trends were compared to yearly snow depths. Years of deep snow and ungulate declines tended to occur in groups. In British Columbia, deep snow appeared to be the major factor limiting mule deer, black-tailed deer, and moose. Clear-cut logging in the Sayward Forest in the late 1940's was accompanied by deer declines. Surviving deer occupied small and scattered patches of timber. Limited information indicated similar trends for Alberta and no conclusive agreement for Alaska. Public acquisition of low elevation winter range was advocated.

26 Egorov, O.V. 1967. Wild ungulates of Yakutia. Israel Program for Scientific Translations, Jerusalem. 204 pp.

(Reindeer/Snow Hardness/Sinking Depth/USSR)

Snow is the environmental factor exerting the greatest influence on wild ungulates of the Yakutia region of Siberia. Snow is loose in Yakutia and does not support even "snow-shoe" type ungulates (reindeer and musk deer). A large hoof surface is detrimental to animals with "stilt" type legs since hooves only slightly submerged in the snow cannot give a sharp strike during flight. In this case, an increase in foot-loading facilitates rapid movement. "Dense snow which carries its weight is more favourable for animals with "snow-shoe" hooves; such

ungulates prefer loose but shallow snow [sic]." The length of the leg and the looseness or density of the snow are of primary importance. An index of ability to move through the snow ("index of passage") is formulated by dividing chest height (cm) by the product of snow depth (cm) and snow density (g/cm^2)[sic]. Reduction of the index implies increased difficulty of movement until a critical region is reached when the snow is strong enough to support the animal. The critical snow density, at depths of chest height, are 0.18-0.20. The critical value for the index of passage is therefore about the same for all ungulates - about 5. The density needed to support an animal ranges from 0.20 in musk deer to 0.40 in wapiti. In Yakutia, snow depths are rarely greater than 30 cm whereas density in early spring is about 0.20. The index of passage therefore varies from 6.7 in musk deer to 16.7 in elk. Normal snow conditions are therefore no obstacle to wild ungulates. Single species accounts of snow relations are then provided for musk deer, wapiti, roe deer, elk (i.e., moose), reindeer, and bighorn sheep.

27 Formozov, A.N. 1946. Snow cover as an integral factor of the environment and its importance in the ecology of mammals and birds. Translated and published by the Boreal Institute, Univ. of Alberta, Edmonton, Alberta, Canada. Occasional Paper No. 1. 141 pp.

(Many Species/Snow Depth, Snow Duration, Snow Hardness/ Mortality, Distribution, Sinking Depth, Food Availability, Movement/USSR)

A rambling, anecdotal and typically-Russian classic. A synthesis of the author's life-long preoccupation with snow. The chapter titled "Snow in Forest Regions" gives Siberian-hunter terminology for snow-types, describes lesser accumulations (by 2-3 times) under the forest canopy, snow compaction in the forest, differential snowmelt rates under canopies and in the open and reviews the early Soviet literature. The chapter titled "Snow Cover as an Obstacle Hindering the Movement of Animals" is largely descriptive and anecdotal; some foot-loadings are given. The influential distinction is made between "chionophobes", "chionophores" and "chionophiles". Snow as a factor influencing migration and snow-related winter mortality is discussed. An extensive treatment is given of the manner in which snow influences the distribution and migration of Soviet mammals and birds.

28 Gaffney, W.D. 1941. The effects of winter elk browsing, South Fork of the Flathead River, Montana. J. Wildl. Manage. 5(4): 427-453.

(Elk/Snow Depth, Snow Hardness/Movement, Food Availability, Distribution/U.S. Mountains)

The amount of snow that elk can negotiate depends on vegetation characteristics, snow characteristics, age and condition of the animals, and topography. Soft snow depths of 30 inches caused elk to shift to browse. Browse plants are raised above the ground and are more available even when buried. Hardpacked snow, 12-24 inches deep may be sufficient to cause a shift to browse. Mature elk moved with difficulty through loose snow 40 inches deep or crusted snow 30 inches deep. The maximum depth elk could tolerate was generally about 48 inches. Calves and weakened adults could not negotiate snow deeper than 30 inches. Topography became an influence when snow depths reached 30 inches. Elk tolerated 12-18 inches more snow on the flats than on a hillside.

29 Gates, J.E., and D.M. Harman. 1980. White-tailed deer wintering area in a hemlock-northern hardwood forest. Can. Field-Natur. 94(3): 259-268.

(White-tailed Deer/Snow Depth/Distribution/Eastern U.S.)

A study of habitat selection by white-tailed deer in Maryland during the unusually severe winter of 1976-1977. Simultaneous measurements were made of trails/ha, beds/ha, pellet groups/ha, basal area/ha, mean canopy cover, wind velocity, and snow depth. An increase in trails was positively correlated with evergreen and total basal area, canopy cover, increased snow depth variability, decreased mean snow depth and decreased wind velocity. Beds showed the same general pattern but no significant correlation with snow conditions. Increased numbers of pellet groups were associated with increases in evergreen and total basal area, canopy cover, decreases in wind velocity and decreased snow depth. Wind velocity decreased with increases in evergreen and total basal area and with canopy cover. Increased snow depth was associated only with wind velocity. Snow depth variability increased with an increase in evergreen and total basal area and decreased with increasing canopy cover.

30 Gilbert, P.F., O.C. Wallmo, and R.B. Gill. 1970. Effect of snow depth on mule deer in Middle Park, Colorado. J. Wildl. Manage. 34: 15-23.

(Mule Deer/Snow Depth/Distribution/U.S. Mountains)

Distribution of mule deer on their winter range in Middle Park, Colorado was largely governed by snow depth. Snow depths > 18 inches precluded use of a range by mule deer. Deer tended to concentrate in localized areas of low snow depth.

31 Gill, J.D. 1957. Review of deer yard management. Maine Dept. Inland Fisheries and Game, Bull. No.5. 61 pp.

(White-tailed Deer//Distribution/Eastern U.S.)

White-tailed deer require timber having a minimum crown closure of 45-70%.

Not seen - cited in Jones (1975).

32 Glasow, W., and E.A. Muller. 1951. Das Gehen auf verschiedenen Boden. Arbeitsphysiologie. 14: 319-321.

(Humans//Sinking Depth, Energy/General)

Reports male humans' energy costs moving over six different surfaces at speeds of 85 to 95 m min^{-1}. Reported energy costs (cal m^{-1} kg^{-1}) were: asphalt road (0.60-0.63); grass path (0.69); potato field furrow (0.83); stubble field (0.85); stubble field ploughed to 10 cm (0.95); field ploughed 18-20 cm deep (1.35). Subjects were wearing 4 kg of clothing including 1.7 kg as laced boots. Authors cite 8 studies giving energy costs of humans as 0.5 cal m^{-1} kg^{-1} at speeds of 3 to 5 km h^{-1}.

Other workers (e.g., Heinonen et al. 1959) have cited this study as giving energy costs of locomotion in snow; that is untrue (but there are some intriguing articles in this journal; e.g., the average German housewife spends 3,000 kcal d^{-1} except on Sundays - 900 to 1,000 kcals).

33 Grinnell, J., and T.I. Storer. 1924. Animal life in the Yosemite. Univ. of California Press, Berkeley. 752 pp.

(Mule Deer, Other Species/Snow Depth/Food Availability/ U.S. Mountains)

As its subtitle states, the book is "an account of the mammals, birds, reptiles, and amphibians in a cross-section of the Sierra Nevada, by two competent natural historians". Its scope leads to anecdotal and second-hand observations.

Regarding mule deer (Odocoileus hemionus hemionus) they noted "The two factors controlling the local distribution of deer in the Yosemite are the presence of the right kind of brush for food and shelter, and the absence of deep snow (p.232)." "When these [preferred] shrubs are covered with snow, or surrounded by snow more than 18 inches deep, the animals are unable to feed. Their [seasonal] altitudinal migrations seem to be entirely controlled by snowfall; they ordinarily remain in the high mountains in the fall until the first snow of the season sends them down hill and concentrates them... As a rule, they do not

stay where the snow lies to a depth of more than 1.5 feet, but, other conditions permitting, they do remain just below this level." And again, "If the first snow is a heavy one the deer leave the altitudes with a rush" (p.233) [a heavy one appears to be 10-12 inches or more].

The authors also show that there are migratory and non-migratory deer populations and that they winter on "sunny, snow-free, south-facing slopes (p.233)."

Commenting on the 'Sierra Nevada Rosy Finch' [currently Grey-crowned Rosy Finch, Leucosticte tephrocotis] the authors note that it has no other birds contesting its habitat [rocky summits, alpine cirques and snowfields], and that it "remains in the cold high country throughout the winter and is well provided with a "snow-mask" over the nostrils (p.431; Fig.51)." [i.e., feathered nares].

34 Hamerstrom, F.N., Jr., and J. Blake. 1939. Winter movements and winter foods of white-tailed deer in central Wisconsin. J. Mammal. 20: 206-215.

(White-tailed Deer/Snow Depth/Distribution/Eastern U.S.)

Deep snow was found not to be a factor in deer yarding in Wisconsin. All other plausible causitive factors were also rejected.

35 Harestad, A.S. 1979. Seasonal movements of black-tailed deer on northern Vancouver Island. Ph.D. thesis, Univ. of British Columbia, Vancouver, B.C. 179 pp.

(Black-Tailed Deer/Snow Depth/Movement, Distribution, Food Availability/Canada West Coast)

The thesis from which the following report was taken.

36 Harestad, A.S. 1979. Seasonal movements of black-tailed deer on northern Vancouver Island. B.C. Fish and Wildl. Res. Rpt. No. R-3. 98 pp.

(Black-tailed Deer/Snow Depth/Movement, Distribution, Food Availability/Canadian West Coast)

A study of home range, migration and habitat use by black-tailed deer on Vancouver Island. Snow depths were measured bi-weekly at 100 m elevation increments along the Mount Cain road. Snow depth increased with elevation. The availability of winter forage was evaluated by estimating the vertical distribution of biomass in forage shrub species and comparing this with snow depths. In unlogged areas, snow depths of 50-110 cm covered 75% of deer food; in logged areas 20-50 cm achieved the same

effect. Deer food availability was also affected by redistribution of the shrubs by snow weight. Vertical compressions, determined by marked twigs, were found to be more than 86%. Prediction equations of available winter food are given for several forested plant associations. Winter ranges were characterized by lesser snow depths and greater food availability. Movements to winter ranges were documented. Forest harvesting at low elevation may have a detrimental effect on winter survival depending upon winter severity, forest type, and availability of alternate habitat.

37 Harestad, A.S., and F.L. Bunnell. 1979. Snow and its relationship to deer and elk in coastal forests. Report to B.C. Council of Forest Industries. 53 pp.

(Black-tailed Deer, Elk/Snow Depth, Snow Hardness/Food Availability, Sinking Depth, Energy/General)

A synthesis paper assessing effects of snow on energy expenditure and acquisition and the effects of forestry practices on snowpack characteristics and winter habitat of deer and elk.

Energy expenditure for movement through a range of depths was determined from a linear regression equation. Sinking depth was calculated as a function of snow density and morphological characteristics. Three-dimensional plots are presented of energy expenditure vs snow density vs snow depth.

Effect of snow on availability of forage is discussed. The major effects of snow on forage availability are a) to exceed vegetation height, b) displace the vegetation down into the snowpack, and c) to allow animals to stand higher above ground level and hence reach previously unavailable browse. The vertical distribution of browse differs between old-growth timber and clearcuts. In dense forest, 50-110 cm of snow is required to cover 75% of the forage whereas only 20-50 cm is sufficient on cutover areas. Litterfall is an important source of food and is enhanced by snow breakage of branches.

Using published data, a regression line is developed relating snow water equivalent in the open to the slope of the snow depth/canopy cover regression. Smaller percentages of snowfall were captured by the canopy in areas of heavier snowfall.

Snow density is an important characteristic as it affects sinking depth. Density of new snow located under tree crowns may be 42% greater than new snow in openings. This may be due to compaction of snow falling from trees. The effect applies only to new snow and snowpack density is relatively unaffected by forest cover.

The dilemma for integrated forestry-wildlife management is that increasing crown closure, while reducing snow depth and energy expenditure for movement, will also reduce understory vegetation.

38 Haugen, A.O., ed. 1971. Proceedings of the snow and ice in relation to wildlife and recreation symposium. Iowa Cooperative Wildlife Research Unit and Iowa State Univ., Ames, Iowa. 280 pp.

(Many Species///General)

A symposium addressing the effects of snow on wildlife. Relevant references are annotated separately.

39 Heinonen, A.O., M.J. Karvonen, and R. Ruosteenoja. 1959. The energy expenditure of walking on snow at various depths. Ergonomics 2: 389-394.

(Humans/Snow Depth/Sinking Depth, Energy/General)

Energy expenditure was measured with a respirometer as human subjects walked through snow of various depths. The results suggested two linear relationships between energy expenditure and sinking depth with an intersection at about 20 cm. Sinking depths of 10,20,30 and 40 cm resulted in energy expenditures of 1.4, 4.1, 8.8 and 12.8 kcal kg^{-1} horizontal in^{-1} respectively. At shallow snow depths, the increase in energy expenditure over walking on firm ground, is less than that required to lift the foot above the snow. At greater depths, the lift alone cannot explain the large difference. The break in the curve corresponds to a shift in the manner of walking. In deep snow, no ballistic movement of the legs is used and the walker assumes a stooped position which contributes to energy expenditure as does the need to balance.

40 Henshaw, J. 1968. The activities of the wintering caribou in northwestern Alaska in relation to weather and snow conditions. Int. J. Biometeorol. 12(1): 21-27.

(Caribou/Snow Depth, Snow Hardness/Cratering, Distribution/Arctic-Subarctic)

When snow depths reach 25 cm, feeding ceased to be a travelling activity and became basically sedentary. Evidence is given for strong selection of local areas with shallow snow depth. In one winter, caribou rarely dug through snow harder than 65 g cm^{-2} whereas in another they chopped through thin layers of 6500 g cm^{-2}. Caribou did not crater through snow deeper than 70 cm and rarely in snow deeper than 50 cm. Potential population numbers are limited more by snow distribution than by food quantity.

41 Hepburn, R.L. 1959. Effects of snow cover on mobility and local distribution of deer in Algonquin Park. M.A. thesis, Univ. of Toronto, Ontario. 55 pp.

(White-tailed Deer/Snow Depth/Eastern Canada/)

A sharp drop in deer mobility occurred as snow depths increased from 25 to 35 cm.

42 Hepburn, R.L. 1978. A snow penetration gauge for studies of white-tailed deer and other northern mammals. J. Wildl. Manage. 42(3): 663-667.

(White-tailed Deer/Snow Hardness/Sinking Depth/Eastern U.S.)

Gives plans for a spring-loaded snow penetration gauge similar to that developed by Verme (1968). The gauge was tested in 588 deer tracks. Two values were recorded; the pressure required to sink the gauge to the depth of the deer track (minimum pressure) and that required to force the gauge further (excessive pressure). The actual foot loading of the deer was assumed to be between these values. The 'best' value for foot-loading of white-tailed deer was determined as 1900 g cm^{-2} or 27 lbs in^{-2}. This loading is several times higher than most cited foot-loading values because it accounts for the dynamic nature of movement.

43 Hershey, T.J., and T.A. Leege. 1976. Influence of logging on summer range in north-central Idaho. Elk-Logging Roads Symp., Univ. Idaho, Pages 73-80.

(Elk/Snow Depth/Distribution/U.S. Mountains)

Up to depths of 50 cm elk seemed to use clear-cuts in direct proportion to snow depth. At greater depths, they dispersed to winter ranges. Clear-cuts were heavily used in spring when snow remained in the forest.

44 Hines, W.W. 1973. Black-tailed deer populations and Douglas-fir reforestation in the Tillamook Burn, Oregon. Oregon St. Game Comm. Res. Rpt. No.3. 59 pp.

(Black-tailed Deer/Snow Depth/Food Availability/ U.S. West Coast)

Snow cover resulted in a shift from a diet of herbs to one almost completely comprised of browse.

45 Hohn, E.O. 1977. The "snowshoe effect" of the feathering on ptarmigan feet. Condor 79: 380-382.

(Other Species/Snow Depth/Sinking Depth/General)

The feathering of ptarmigan feet has been considered as a "snowshoe" adaptation since at least the late 19th century. Recently, the function has been termed a "children's book error". The author measured the surface area, loading, and sinking depths of feathered and unfeathered feet. Foot feathering increases the bearing surface by four times and reduces sinking depth by a half.

46 Hosley, N.W. 1956. Management of white-tailed deer in its environment. Pp. 187-259 in: W.P. Taylor, ed. The deer of North America. The Stackpole Co., Harrisburg, PA. 668 pp.

(White-tailed Deer/Snow Depth/Movement/Eastern U.S.)

Snow depths greater than about 20 inches make white-tailed deer travel by jumps. Height of fawn's breast is 18-19 inches vs 20-22 for an adult.

47 Hungerford, K.E. 1964. Availability of deer browse under varying snow conditions. Idaho Coop. Wildl. Res. Unit Quart. Rpt. 17(4): 1.

(Mule Deer/Snow Depth/Food Availability/U.S. Mountains)

When snow depths reached 75 cm, 23% of current annual growth of "Ceanothus shrubs" in Idaho were available. Western red cedar, ranging in height from 7 to 10 feet, had 46% and 42% of total branch length available at snow depths of 68 cm and 66 cm respectively.

48 Huot, J. 1974. Winter habitat of white-tailed deer at Thirty-One Mile Lake, Quebec. Can. Field-Natur. 88(3): 293-301.

(White-tailed Deer/Snow Depth/Distribution, Food Availability/Eastern Canada)

Deer preferred to remain in conifer-intolerant hardwood forest, cedar-balsam-spruce forest, pine forest and intolerant hardwood-conifer forest. Conifer swamps and tolerant mixed woods were less favoured. The types producing most forage were intolerant hardwood-conifer, cedar-balsam-spruce, and the conifer-tolerant hardwood types. Conifer swamps, hardwood stands, and openings were least productive. Preference for protective cover for bedding increased through the winter, into February. Favoured bedding types were hemlock and conifer-intolerant hardwoods. There was a strong preference for bedding on level ground near large conifers. Deer tended to bed in areas of lesser snow depths. Deer avoided recent clear-

cuts and used semi-open forest which represents a compromise between shelter and food requirements.

49 Jacobsen, N.L.K. 1973. Physiology, behavior, and thermal transactions of white-tailed deer. Ph.D. thesis, Cornell Univ., New York. 346 pp.

(White-tailed Deer/Snow Depth/Energy/Eastern U.S.)

A study of the behaviour, energetics, and physiology of white-tailed deer as these are influenced by seasonality. Heart rate was used as an index of energy expenditure. Pages 218-223 deal with the effect of snow on heart rate and energy expenditure during activity. During pawing of snow, heart rates averaged 57 bpm over mean monthly heart rate, corresponding to energy expenditures of 61-176 kcal hr^{-1}. Energy expenditure during pawing was approximately linear to snow depths of 15 cm and thereafter increased rapidly. In 20 cm of snow, pawing was 3.5 times as costly as standing. Walking through snow 2.5 cm deep entailed energy expenditures of 109 kcal hr^{-1} whereas snow 44 cm deep required an expenditure of 215 kcal hr^{-1}.

50 Janson, R. 1973. Administration Region 2. Proc. West. States Elk Workshop, Bozeman,.Montana.

(Elk/Snow Hardness/Distribution//U.S. Mountains)

Crusted snow may prevent elk from using grasslands. During such periods, they remain and feed in timbered areas.

Not seen - cited in McLellan (1978).

51 Jones, G.W. 1975. Aspects of the winter ecology of black-tailed deer (Odocoileus hemionus columbianus Richardson) on northern Vancouver Island. M.Sc. thesis, Univ. of B.C., Vancouver. 78 pp.

(Black-tailed Deer/Snow Depth, Snow Hardness/ Distribution, Food Availability/Canadian West Coast)

A study of winter ecology of black-tailed deer in the Nimpkish Valley of northern Vancouver Island designed to determine the effects of clearcut logging on deer winter range.

Snow depths increased with increasing elevation in both logged and unlogged areas. Snow depths in the forest were about half as great as in clearcuts. Snow depth in feet (y) was related to crown closure in % (x) by the expression $y = 5.69 - 0.07x$. Crown closure decreased with

increasing elevation whereas Vaccinium and cedar decreased in abundance with increasing canopy cover. Vegetative cover cannot be predicted from seral type, elevation, aspect or crown closure.

In severe winters, diets were composed primarily of conifers and shrubs and are less diverse than in mild winters. Deer use of logged habitat was low when the snow was deep and soft and increased when the snow became crusted. This increase was most noticeable in second growth slash where browse was available. Track counts were not statistically well correlated with track depth or snow depth which contradicted subjective conclusions. Only timber habitats having crown closures of $\geq$ 65% were heavily used. Deer use was greater in timbered habitat having a shrub understory than in habitats having a conifer understory.

Chest heights, total foot areas, and foot loadings are presented. It is recommended that heavily-used winter ranges be excluded from logging plans.

52 Kelsall, J.P. 1969. Structural adaptations of moose and deer for snow. J. Mammal. 50: 302-310.

(Moose, White-tailed Deer/Snow Hardness/Sinking Depth/ Eastern Canada)

Measurements of chest height, live weight, track area and weight-load of deer and moose from New Brunswick and Nova Scotia. Male deer have higher foot loadings than the females. There were few measurements for female moose so a between-sex comparison could not be made. Chest heights were 47-71 cm for deer and 80-117 cm for moose. Deer were restricted by 40 cm of snow; moose by 70-99 cm. When snow depths reached 24 cm, deer moved to lower elevations. About 3/5 of an ungulate's weight is borne on the front feet which may be 20% larger than the hind ones. Weight-loadings were more or less the same for deer and moose. The support given by snow hardness is complex. Crusts of great hardness (e.g., 70,000 g cm^{-2}) have been observed to be inadequate to support ungulates.

53 Kelsall, J.P., and W. Prescott. 1971. Moose and deer behaviour in snow. Canadian Wildlife Service Rept. Series 15. 25 pp.

(Moose, White-tailed Deer/Snow Depth, Snow Density, Snow Hardness/Distribution, Sinking Depth/Eastern Canada)

A study of snow characteristics in relation to moose and deer behaviour in Fundy National Park. In three winters, there was 45% less snow under forest canopies than in the open. Snow was always deeper on moose range than on deer

range. Deer avoided open areas, unless windblown, and, where depths exceeded 40 cm, favoured well-established trails. Only a few large bucks remained at higher elevations. Travelling moose remained under forest canopies; this tendency increased with increasing snow depths. At depths > 97 cm, moose were rarely seen except in the trees. It is suggested that 70 cm is a critical snow depth for moose in Fundy National Park due to poor browse conditions. Moose and deer sink about equally far into snow of different densities but deer are more easily impeded because of their smaller chest heights. Snow hardnesses were almost always lower under the canopy than in the open. Fewer crusts were found on deer range; probably as a function of lower elevation. It was difficult to reconcile the theory of ungulate support by snow crusts with available data. Crusts were rarely consistent enough to permit unhindered travel. Track depths for both moose and deer were consistently greater by a factor of 25-76% in the open than under the canopy.

54 Kelsall, J.P., and E.S. Telfer. 1971. Studies of the physical adaptation of big game for snow. Pp. 134-146 in: A.O. Haugan, ed. Proc. of snow and ice in relation to wildlife and recreation symp. Iowa State Univ., Ames, Iowa. 280 pp.

(Moose, Bison, Elk, White-tailed Deer//Sinking Depth, Foot Loading/Canadian Mountains)

Presents standardized methods for determining chest heights, hoof area, foot area and foot loading from dead animals. Data are presented from > 400 moose, elk, bison and white-tailed deer slaughtered in Elk Island and Jasper National Parks. Young animals had smaller foot loadings. Bison had the greatest foot loading and relatively short legs, and were least adapted to deep snow. White-tailed deer had the smallest foot loads. Foot loading increased linearly with chest height within species.

55 Kelsall, J.P., E.S. Telfer, and K. Simpson. 1980. Indirect determination of ungulate foot area. Can. J. Zool. 58: 464-466.

(White-tailed Deer, Bison, Elk, Moose//Sinking Depth, Foot Loading/Canada Mountains)

Hoof width times foot length is an index which predicts actual foot area with correlation coefficients of 0.94 - 0.99 in white-tailed deer, elk, moose and bison. No significant differences were found between males and females in foot area.

56 La Pierre, A.J., and P.C. Lent. 1977. Caribou feeding sites in relation to snow characteristics in northeastern Alaska. Arctic 30(2): 100-108.

(Caribou/Snow Depth, Snow Hardness/Distribution, Food Availability/Arctic-Subarctic)

Ram hardnesses and snow depths were measured inside and outside of caribou feeding areas. Snow depths and ram hardnesses were less in cratered areas than in adjacent sites. Caribou selected areas of shallow snow (< 50 cm) for winter feeding and did so on broad microsite scales. The hardness of the snow affected feeding but in a complex manner. Most winter ranges had ram hardnesses < 85 cm whereas unused areas had harder snow. However, they did feed in areas with shallow, hard, slab-like crusts.

57 Leader-Williams, N., T.A. Scott, and R.M. Pratt. 1981. Forage selection by introduced reindeer on South Georgia, and its consequences for the flora. J. Appl. Ecol. 18: 83-106.

(Reindeer/Snow Depth, Snow Hardness/Food Availability/ Antarctic)

A study of the relationships of reindeer and the flora of a subanarctic island. Snow depth was measured monthly with aluminum snow-poles. Snow hardness was measured with a Ramsonnde penetrometer. Forage was considered to be unavailable to reindeer if snow depths exceeded 60 cm or mean snow hardness was greater than 22 kg. The "tussock grassland" type was the only community available throughout the winter. Almost all feeding occurred there during mid-winter. Diet diversity was inversely correlated with snow depth. Snow cover may protect the diversity of the flora on South Georgia and seems to keep caribou populations low in number and stable by causing a large seasonal reduction in carrying capacity.

58 Leege, T.A., and W.O. Hickey. 1977. Elk-snow-habitat relationships in the Pete King Drainage, Idaho. Idaho Dept. Fish and Game Wildl. Bull. 6. 23 pp.

(Elk/Snow Depth/Distribution/U.S. Mountains)

In Idaho, 93% of elk were concentrated on 27% of a drainage where snow was less than 61 cm deep. Snow depths were greatest on north aspects and less under mature trees than in brushfields.

Not seen - cited in McLellan (1978).

59 Lent, P.C. 1974. Ecological and behavioral study of the Nunivak Island muskox population. Unpubl. Rpt. on file Alaska Coop. Wildl. Unit, Univ. of Alaska, Fairbanks.

(Reindeer/Snow Depth, Snow Hardness/Food Availability, Distribution/Arctic-Subarctic)

Reindeer exhibited micro-relief selection on Nunivak Island. Snow depths at craters averaged 21 cm whereas depths at randomly selected adjacent sites averaged 56 cm. Mean snow hardness was greater at uncratered sites.

Not seen - cited in LaPierre and Lent (1977).

60 Lent, P.C., and D. Knutson. 1971. Muskox and snow cover on Nunivak Island, Alaska. Pages 50-57a in: A.O. Haugen (ed.), Proc. Snow and Ice in Relation to Wildl. and Recr. Symp., Iowa St. Univ., Ames. 280 pp.

(Muskoxen/Snow Depth, Snow Hardness/Distribution/Arctic-Subarctic)

A study of muskox distribution on Nunivak Island in relation to snow depth and hardness as determined by a Ramsonnde penetrometer. A description of the Ramsonnde, its use, and its advantages is provided. Integrated ram profiles are expected to provide an index of the amount of work necessary to dig through the snow layers. Muskoxen feed primarily in areas with little or no snow.

61 Leopold, A., T. Riney, R. McCain, and L. Tevis. 1951. The Jawbone deer herd. Calif. Fish and Game Bull. No. 4. 139 pp.

(Mule Deer/Snow Depth/Mortality/U.S. Mountains)

Snow depths of 4 ft are disastrous for mule deer.

Not seen - cited in Jones (1975).

62 Loveless, C.M. 1967. Ecological characteristics of a mule deer winter range. Colorado Game Fish and Parks Dept. Tech. Publ. 20. 124 pp.

(Mule Deer/Snow Depth, Snow Duration, Climate/Distribution, Movement/U.S. Mountains)

A comprehensive and detailed treatment of mule deer winter range in the Front Range, north-central Colorado. Unfortunately, "It is obvious that environmental data... cannot be mathematically correlated with deer behavioural patterns." (p.87). [There were no continuous, quantitative records of deer activity and

movement patterns].

Relevant comments include: "mule deer on the study area showed perhaps more response to snow depth than any other single weather element with the possible exception of interacting air temperature and atmospheric moisture." (p.92). Locations with greatest deer use were south- and west-facing exposures and a ridge which had shallow snow depths.

"Ground-surface snows of 10-12 inches [25-30 cm] seemingly impeded the movements of deer, especially yearlings, and depths of 20 to 24 inches [50-60 cm] essentially precluded the animals' use of an area and seriously hampered or prevented locomotion". (p.92).

Although detailed correlations could not be drawn, the study is a classic treatment of winter range and is well worth reading before designing a winter range study.

63 Lundgren, N., V. Sundberg, and A. Lindholm. 1955. A study of the heaviness of work in using power saws in timber cutting. (Swedish with English summary). Medd. Skogsforskn. Inst. Stockh. 45(10): 1-46.

(Human/Snow Depth/Energy/General)

Depths of snow are indicated but not sinking depths. Walking through 5 to 10 cm of snow was associated with 1.6 times as much energy expenditure as walking on a road. Snow 32-42 cm deep resulted in energy expenditures of 2.45 cal kg^{-1}. horizontal m^{-1}.

Not seen - cited in Heinonen et al. (1959).

64 Mattfeld, G.F. 1973. The effect of snow on the energy expenditure of walking white-tailed deer. Trans. Northeast Fish and Wildl. Conf. 30: 327-343.

(White-tailed Deer//Energy/)

A shorter version of Mattfeld (1974) containing the most pertinent bioenergetic work.

65 Mattfeld, G.F. 1974. The energetics of winter foraging by white-tailed deer -- a perspective on winter concentration. Ph.D. thesis, St. Univ. of New York, Coll. Env. Sci. and For. 306 pp.

(White-tailed Deer//Energy/)
An attempt to determine how the depth, density and hardness of the snow cover influences the energy expenditure of locomotion of white-tailed deer. Energy

expenditures of deer were measured using indirect calorimetry. Some deer were intractable and had to be drugged. The relationship between energy expenditure and sinking depth, based on 214 determination was logarithmic and expressed as log Y (kcal kg^{-75} m^{-1}) = 0.00925 sinking depth (SD) in cm + 0.00019 SD^2 - 2.2234. The rapid increase in energy expenditure occurs at depths of approximately 30 cm. The chosen speed of travel decreased with sinking depth and was expressed by log (ft min^{-1}) = 2.570 - 01168 x SD with a correlation coefficient of - 0.57. Deer adjusted their speed to equalize energy output per unit time. Energy expenditure was 11.97 kcal/min while plunging through snow and 10.17 Kcals min^{-1} while walking. At the same time, energy expenditure per 100 ft walked was 6.99 kcal vs 13.19 kcal for plunging. Lifting the body and legs clear of the snow appears to be the primary factor responsible for high energy expenditure although humans walking on bare ground with exaggerated leg lifts exhibited only moderate energy increases. This suggests that the inability to swing the legs through the snow is instrumental. Slippage and the need to balance may also be significant. A dynamic loading procedure was used to characterize the ability of crusts to support deer. This consisted of a lead-weighted steel bar with a cross-sectional area of 19.24 cm^2 and weighing 1 kg which was dropped from 10, 40, and 80 cm. The SE's were very high. A regression model indicated that energy expenditure per m appeared to be most dependent upon a momentum term and sinking depth or its apparent analogy, the 80 cm drop weight. There was a negative relationship with the 10 cm drop because large values indicate fluffy snow which permits wading. Large sinking depths decreased the expenditure per unit distance because fluffy snow allowed greater velocities. There was no way to determine whether plunging was more efficient than walking in any particular snow type. Mean snow depths over 9 years were calculated for 6 Adirondack locations. Sinking depths, snow depths, and forage availability were calculated for hardwood and coniferous forest types. It was suggested that coniferous forests represent a more favourable compromise between energy input and output.

66 McLellan, B. 1978. Relationships between elk, snow, habitat use, and timber management in the White River drainage of southeastern British Columbia. Unpubl. ms., 33 pp.

(Elk/Snow Depth/Distribution/Canadian Mountains)

A study of winter habitat preferences by elk in southeastern British Columbia. Snow depths averaged 22% less on south-facing clear-cuts than on level ones. In the forest, snow depths were less but snow lasted longer in the spring. Denser immature pine forest had less snow than the mature forest. The selectively cut areas had the

most snow throughout the winter. Elk group size was inversely related to snow depth, because elk kept to the forest during deep snow periods. Elk moved less during periods of deep snow. Elk used clear-cuts only rarely when snow depths were > 48 cm. There was no clear change in elk use associated with snow depth in selectively cut areas, but the least number of tracks were seen when snow was the deepest. Over the entire winter, the selective cut was used more than were the clear-cuts. Use of timbered areas was reasonably constant throughout the winter. The riparian areas were the most heavily used. Recommendations are made for acceptable logging practices.

67 Meagher, M.M. 1971. Snow as a factor influencing bison distribution and numbers in Yellowstone National Park. Pages 63-67 in: A.O. Haugen (ed.). Proc. Snow and Ice in Relation to Wildl. and Rec. Symp., Ames, Iowa.

(Bison/Snow Depth/Distribution, Food Availability, Mortality/U.S. Mountains)

Bison wintering in the Pelican Valley of Yellowstone Park were subjected to more severe snow conditions than elsewhere in the park. With snow depths of 40-45 inches, bison fed primarily in sedge bottoms. As snow depths increased, groups scattered and began to use wind-scoured benches and slopes. This appeared to occur when snow depths reached 50-60 inches. When snow depths exceeded 60 inches, bison moved to small thermal areas and used the snow wells at the base of trees. Large decreases in bison numbers occurred during severe winters when population numbers exceeded 200. Bison were able to endure more severe snow conditions than other large mammals in Yellowstone largely because of their ability to forage through deep snow.

68 Meagher, M.M. 1973. The bison of Yellowstone National Park. U.S. Natl. Park Serv. Sci. Monogr. Ser. No. 1: 1-161.

(Bison/Snow Depth/Distribution, Food Availability/ U.S. Mountains)

Under normal conditions, snow depth does not limit forage availability to bison. In conditions of severe snow depth or high population levels it may become a limiting factor. Bison swing their heads in a sideways motion to clear deep snow. Deep snow significantly limited bison movements.

69 Mech, L.D., L.D. Frenzel, Jr., and P.D. Karns. 1971. The effect of snow conditions on the vulnerability of white-tailed deer to wolf predation. In: L.D. Mech and L.D. Frenzel (eds.), Ecological studies of the timber wolf

in northeastern Minnesota. USDA For. Serv. Res. Paper No. NC-52. 62 pp.

(Wolves, White-tailed Deer/Snow Depth, Snow Hardness/ Mortality, Sinking Depth/Eastern U.S.)

Snow depth and penetrability (measured with Verme's 1968 apparatus) were measured over 3 winters. The winters 1966-1967 and 1967-1968 were characterized by normal or less than normal snow accumulations. The winter of 1968-1969 was characterized by deep snow, high penetrability until January, then a rapid decrease in penetrability. In January, deer sank in 2.5 - 3.5 feet. Later, as penetrability decreased, deer still had trouble in moving since support was not adequate for running and the denser snow offered more resistance. Wolves had a much easier time catching deer in February - March 1969. As snow became extremely deep, wolves gained an advantage because of a lesser weight-load-on-track. The high snow density accentuated this difference.

70 Miller, F.L. 1970. Distribution patterns of black-tailed deer (Odocoileus hemionus columbianus) in relation to environment. J. Mammal. 51: 248-260.

(Black-tailed Deer/Snow Depth/Distribution, Food Availability/U.S. West Coast)

Six inches of snow altered the feeding patterns of deer by covering most trailing blackberry and grass. When snow depths were great, deer remained on ridges 200-400 ft above drainage bottoms where there was an abundant supply of woody browse plants. During January, Vaccinium and Gaultheria sites between 1200-1500 ft were among the first to have open ground and were utilized by deer. As lower elevations became clear, deer moved down to feed on trailing blackberry; during deep snow periods, deer utilized Douglas fir as survival food.

71 Moen, A.N. 1973. Wildlife ecology: An analytical approach. W.H. Freeman and Co., San Francisco. 438 pp.

(White-tailed Deer/Snow Depth/Food Availability/Eastern U.S.)

Contains a section on snow cover in relation to kinetic energy primarily as an example of how to proceed with model building. In an upland hardwood forest in New York, one foot of snow rendered 97% of deer forage unavailable. In a zone of invading plants between a hemlock stand and an abandoned field, one and two feet of snow reduced forage availability by 25 and 40% respectively.

72 Moen, A.N., and K.E. Evans. 1971. The distribution of energy in relation to snow cover in wildlife habitat. Pages 147-162 in: A.O. Haugen (ed.), Proc. Snow and Ice Symp. in Relation to Wildl. and Rec., Ames, Iowa. USDA For. Serv. Res. Paper PSW-18. 24 pp.

(White-tailed Deer/Snow Depth, Climate/Energy, Food Availability/General)

Very similar to the treatment of snow in Moen (1973). Reviews the physical properties of snow, windpacks, windbreaks, canopy effects, radiation, thermal balance of animals, and snow as a mechanical barrier to animals.

73 Moran, R.J. 1973. The Rocky Mountain elk in Michigan. Michigan Dept. Nat. Resources, Res. and Dev. Rpt. 267.

(Elk/Snow Depth/Food Availability/Eastern U.S.)

Snow cover resulted in a shift in diet from herbs and grasses to one almost completely comprised of browse.

74 Morrison, P.R. 1966. Biometeorological problems in the ecology of animals in the Arctic. Int. J. Biometeor. 10: 273-292.

(Many Species//Movement/General)

A review of the effects of arctic weather on animals with emphasis on the Soviet literature. Contains a section titled "Behavioural Implications of Snow".

75 Nasimovich, A.A. 1955. The role of the regime of snow cover in the life of ungulates in the U.S.S.R. Muskva, Akad. Nauk ASSR, 403 pp. Transl. from Russian by the Canadian Wildlife Service, Ottawa, Canada.

(Many Species/Snow Depth, Snow Hardness/Sinking Depth, Mortality, Distribution, Movement, Food Availability/ USSR)

The most ambitious compendium of the effects of snow on ungulates presently available. Chapter I deals with movement of ungulates through snow. Figures 1 and 2 give foot-loadings and chest heights respectively. Animals are separated into "snowshoe-ungulates" (musk deer and reindeer), "stilt-walkers" and "rock-climbers". Critical depths are given in the species-by-species discussion. The effects of snow crusts on movement are discussed.

Chapter II deals with the effect of snow on ungulate diets. Ungulate species are broken down by the class of forage eaten. The diversity of the winter diet is almost

invariably lesser than the summer diet. Ungulates can forage through deeper snow if it is lower density. Reindeer are the most proficient of ungulates in obtaining food from beneath the snow. The winter feeding of many wild and domestic ungulate species is described in some detail.

Chapter III deals with the effect of snow cover on the winter distribution of ungulates. Mountainous areas have the most variability in snow depth and therefore offer the widest choice of habitat selection. Animals often contract their home ranges in winter.

Chapter IV deals at great length with seasonal migrations of ungulates due to snow conditions.

Chapter V discusses intra- and inter-specific relations of ungulates during snowy seasons. In most ungulates, gregariousness is more marked in the winter. Predators gain an advantage over ungulates due to their generally smaller weight-loads-on-track. Table 5 lists weight-loads for predator species. This advantage is to some extent offset by the generally shorter legs of predator. Wolves therefore avoid taiga forests where the snow is deep and powdery; the critical depth is 50 cm.

Chapter VI deals with the effect of snow on ungulate mortality.

Chapter VII treats the effect of snow cover on the configuration of ungulate ranges and ungulate distribution. Hunting can be particularly destructive during winters of deep snow.

76 Ozoga, J.J. 1968. Variations in microclimate of a conifer swamp deer yard in northern Michigan. J. Wildl. Manage. 32: 574-589.

(White-tailed Deer/Snow Depth, Snow Hardness/ Distribution, Sinking Depth, Food Availability/Eastern U.S.)

Six habitat types within a Michigan conifer swamp were sampled for humidity, temperature, wind, snow depth and snow hardness. A densely stocked even-aged stand of mature swamp conifers offered deer the best protection; here, thermal ranges were narrowest, average temperatures warmest, relative humidity highest, wind lowest, snow depths least and snow support best. Pole-sized conifers, although equally dense, did not reduce snow depth as much. Snow support was measured using the compaction gauge developed by Verme (1968). Poorest support was found in the sapling conifers. On average, snow support values in the mature conifer were 31% better than in hardwood stands and 22-23% better than in open, mixed and pole-sized

conifers. No site provided optimal shelter as well as adequate food. Openings adjacent to the yards lost snow the fastest and were visited as soon as snowmelt had progressed far enough. It is recommended that shelter areas be maintained interspersed with food producing areas.

77 Ozoga, J.J., and L.W. Gysel. 1972. Response of white-tailed deer to winter weather. J. Wildl. Manage. 36: 892-896.

(White-tailed Deer/Snow Depth, Climate/Distribution/ Eastern U.S.)

Deer movements within a conifer swamp were measured with traffic counters and trip recorders. Deer activity in the swamp increased dramatically as temperature got colder and wind chill increased. Since deer were less active during periods of cold, this observed relationship was felt to be a function of deer moving into thermal cover. Cold is felt to be the major factor in driving deer into protective cover rather than snow.

78 Passmore, R.C. 1953. Snow conditions in relation to big game in Ontario during the winter of 1952-53. Ontario Dept. Lands and Forests, Wildl. Res. Rept. 2. 12 pp.

(White-tailed Deer/Snow Depth, Snow Hardness//Eastern Canada)

Establishment of a network of snow stations to record weekly snow depth and crust conditions and to evaluate the effect of these factors on deer.

Not seen - cited in Hepburn (1978).

79 Peek, J.M. 1971. Moose-snow relationships in north-eastern Minnesota. Pp. 39-45 in: A.O. Haugen, ed. Proc. of snow and ice in relation to wildlife and recreation symp. Iowa Cooperative Wildlife Research Unit and Iowa State Univ., Ames, Iowa. 280 pp.

(Moose/Snow Depth, Snow Hardness, Snow Density/ Distribution/Eastern U.S.)

A study of moose habitat-use in relation to snow characteristics in Minnesota. Snow depth, density and hardness were measured at 30 day intervals in 6 forest cover types. Snow hardness and depth were greater in the open whereas there was no effect of cover type on snow density. When a differential in depth and hardness occurred, moose shifted to denser stands.

80 Peek, J.M. 1971. Moose habitat selection and relationship to forest management in northeastern Minnesota. Ph.D. thesis. Univ. of Minnesota, St. Paul. 250 pp.

(Moose/Snow Depth/Distribution/Eastern U.S.)

There were no consistent differences in snow depth attributable to stand height.

Not seen - cited in Eastman (1978).

81 Peterson, R.O., and D.L. Allen 1974. Snow conditions as a parameter in moose-wolf relationships. Naturaliste Can. 101: 481-492.

(Moose, Wolves/Snow Depth, Snow Hardness/Sinking Depth, Mortality/Eastern U.S.)

A study of wolf-moose relationships in relation to snow conditions on Isle Royale. Snow hardness was measured with a compaction gauge comprising a 1.98 cm^2 area statically loaded with up to 650 g cm^{-2}. Overstory was found to decrease snow depth by 29% in one plot and 15% in another. Penetration was 30% greater under the canopy. A total of 220 fresh tracks of 17 moose were measured and an average foot-loading of 230 g cm^{-2} was determined. This is less than the 420-1000 g cm^{-2} reported in other studies. Wolves were found to have foot loadings of 100 g cm^{-2}. Significantly more moose were killed in areas of > 51 cm snow depth. During deep snow periods, both moose and wolves used shorelines for travel and encountered each other more frequently. More calves were killed when snow depths were > 76 cm.

82 Peterson, R.O. 1977. Wolf ecology and prey relationships on Isle Royale. U.S. Dept. Interior Natl. Park Service Monogr. Ser. No. 7. 210 pp.

(Wolves, Moose/Snow Depth/Sinking Depth, Mortality, Distribution/Eastern U.S.)

Wolves have lower foot loadings than do moose - published data are reviewed. Moose rarely receive consistent support from snow crusts whereas wolves often do. Wolves have short legs and sink deeply in snow of low density; they often travel single file through such snow. In 1971, 41 cm of snow over a 51 cm base precluded extensive wolf travel over the interior of the island. The following year, when snow depths were 75 cm, wolves were usually limited to shorelines. Increased kill rates of moose occurred in winters of deep snow. When snow depths exceeded 75 cm, calf kills became more frequent. Kills along shorelines become more frequent with increasing snow depth. Conifer cover became important to moose as snow

accumulated. Recent burns attracted moose despite deep snow. With snow depths exceeding 50 cm, more moose kills occurred near shorelines and fewer in the burns.

83 Petocz, R.G. 1973. The effect of snow cover on the social behavior of bighorn rams and mountain goats. Can. J. Zool. 51: 987-993.

(Bighorn Sheep, Mountain Goats/Snow Depth/Energy/ Canadian Mountains)

The social behavior of bighorn rams was studied during deep snow and shallow snow winters. Snow depth had no effect on the intensity of bighorn social activity during the rut. Deep snow reduced the number of post-rut social interactions in bighorn rams but not in mountain goats. Under extreme snow conditions, rams exhibited an increase in overt aggressive behavior and a reduction in dominance displays.

84 Picton, H.D., and R.R. Knight. 1971. A numerical index of winter conditions of use in big game management. Proc. Snow and Ice Symposium, Iowa St. Univ., Ames, pp. 29-38.

(Elk/Snow Depth/Distribution/U.S. Mountains)

Description of a low cost winter severity index based on Weather Bureau records. Daily maximum temperature (^{o}F) above or below freezing were multiplied by number of inches of snow on the ground. Maximum elk counts were associated with winters with high index ratings due to greater concentration on winter range.

85 Popotov, R.A. 1969. [The functional importance of the horny fringe on the toes of black grouse]. Zool. Zh. 48(9): 1379-1382 (in Russian)

(Other Species/Climate/Sinking Depth/USSR)

A discussion of foot loading in grouse. The black grouse is contrasted with other grouse of "snowless" regions.

86 Popov, S.P. 1957. Deer transport for the game industry. In: Improvement of the Game Industry. 6th. ed., Izd. Tsentroyvza, Moscow.

(Other Species//Sinking Depth/USSR)

Includes a discussion of foot loading as determined by dividing foot area by body weight. The "white hare" has a static foot loading of 8.4 to 11.8 g cm^{-2}.

Not seen - cited in Burdukov and Kozlov (1979).

87 Prescott, W.H. 1968. A study of winter concentration areas and food habits of moose in Nova Scotia. M.Sc. thesis, Acadia Univ. 194 pp.

(Moose/Snow Depth/Distribution/Eastern Canada)

Snow depths in the 60-70 cm range restricted the mobility of moose.

Not seen - cited in Telfer (1970).

88 Pruitt, W.O., Jr. 1959. Snow as a factor in the winter ecology of the barren-ground caribou. Arctic 12: 159-179.

(Caribou/Snow Depth, Snow Hardness/Distribution, Movement, Sinking Depth, Cratering/Arctic-Subarctic)

Areas of caribou concentration were characterized by hardnesses of 6.5-6.0 gm cm^{-2} for forest stations and 50-700 gm cm^{-2} for lake stations. The density range was 0.13-0.20 for forest stations and 0.13-0.32 for lake stations. Hardnesses and densities were often greater in areas not frequented by caribou. The threshold of sensitivity to hardness is about 50 gm cm^{-2} in the forest and 500 gm cm^{-2} for lakes. Density thresholds are 0.19-0.20 for forests and 0.25-0.30 for lakes. The depth threshold seems to be about 60 cm. Caribou will crater an area twice and were observed to dig 366 craters $acre^{-1}$ each time. Lakes were used as escape or loafing cover. Bands usually bedded down 75-100 yards from shore which was the approximate wind shadow distance. Caribou movements and groupings were constrained by "fences" of unfavorable snow. Caribou hoofs are larger in winter due to abrasion in summer. A glossary of specialized snow terms is appended.

89 Pruitt, W.O., Jr. 1960a. Animals in snow. Sci. Am. 202(1): 60-68.

(Many/Snow Depth, Snow Hardness/Distribution, Energy, Mortality/General)

Discusses the metamorphosis of snow into categories described by aboriginal snow terms. A glossary of these terms is included. The critical hardness and depth of tundra snow to caribou are 60 g cm^{-2} and 2 ft respectively. Caribou movements are constrained by "fences" of snow with unfavourable characteristics. Moose have adapted to snow by developing long legs. Snow depths of about 3 feet are critical for moose. The alternative to the moose's "stilt" adaptation is the hare's snowshoe

adaption. Small animals, with unfavourable surface-volume ratios must live beneath the snow surface. Pleistocene megafaunal extinctions may have been due to increased snowfalls.

90 Pruitt, W.O., Jr. 1960b. Behavior of the barren-ground caribou. Biol. Pap. Univ. Alaska No. 3. 44 pp.

(Caribou/Snow Depth, Snow Density, Snow Hardness/ Distribution, Cratering, Movement/Arctic-Subarctic)

Includes a section entitled "Behavior during Snow Season". Cratering behavior is described. Snow "sets" more quickly at cold temperatures and caribou therefore shift their feeding grounds more frequently when it is cold. Caribou can walk on a surface layer with a hardness of 1,500 g cm^{-2}. Caribou use lakes as "escape cover" because snow depths there are less. They bed 70-90 m from shore which is approximately the extent of the "wind shadow". The threshold of nival tolerance seems to be 50 g cm^{-2} for forest snow and 500 g cm^{-2} for lake snow. Snow depths of 60 cm seem critical.

91 Pruitt, W.O., Jr. 1966. Ecology of terrestrial mammals. Pages 519-564 in: N.J. Wilimovsky and J.N. Wolfe (eds.), Environment of the Cape Thompson Region, Alaska. USAEC Div. Tech. Info. PNE-481.

(Other Species/Snow Depth, Snow Hardness/Distribution/ Arctic-Subarctic)

A snow index was calculated as layer thickness (cm) times density summed over all layers. Very few small mammals were found under snowpacks with snow indices > 10 and none were found under snowpacks with indices < 1.

92 Pruitt, W.O., Jr. 1971. Report on international workshop on Rangifer winter ecology, Vittangi, Sweden. 20-26 March. 5 p.(mimeo).

(Reindeer-Caribou/Snow Depth, Snow Hardness, Climate/ Cratering/General)

A privately circulated report (FLB reprint #512) that includes little that is not in Pruitt (1971b).

93 Pruitt, W.O., Jr. 1971b. Scandinavian-Canadian field workshop on Rangifer-Snow ecology. Arctic 24(2): 145.

(Reindeer-Caribou///General)

Report of an informal meeting of reindeer and caribou

biologists in Finland. Includes a list of recommendations for further study of Rangifer - snow interactions.

94 Pruitt, W.O., Jr. 1979. A numerical "snow index" for reindeer (Rangifer tarandus) winter ecology (Mammalia, Cervidae). Ann. Zool. Fennici 16: 281-285.

(Reindeer/Snow Hardness, Snow Depth/Distribution/Europe)

Presents development of a mathematical index relating distribution of Finnish reindeer to features of the snow cover. The Varrio Snow Index (VSI) incorporates hardness of the hardest layer in the upper half of the snow cover, the hardness and thickness of the basal layer, the vertical hardness of the snow cover surface, the thickness of the topmost layer, the hardness and thickness of the hardest layer, and the total thickness of the snow cover. The VSI predicted reindeer distribution well. Includes a glossary of specialized snow terminology from several languages.

95 Pulliainen, E. 1974. Seasonal movements of moose in Europe. Naturaliste Can. 101: 379-392.

(Moose/Snow Depth/Distribution/Europe)

A review of the literature on European moose migrations. It is concluded that moose winter range is characterized by sufficient food reserves but not necessarily by low snow depth.

96 Pullianen, E. 1980. Hivielainten talviset liikunnot ja ravinnonotto [Winter diet and movements of cervids. A review]. Memoranda Soc. Fauna Flora Fennica 56: 51-58 (in Finnish).

(White-tailed Deer, Moose, Reindeer, Other Ungulates, Wolves/Snow Depth/Distribution, Food Availability, Cratering, Foot Loading/USSR, Europe)

If my [FLB] Finnish is correct this paper presents little new information, but collates other published work. Results of several food habit studies in regions with >40cm snowfall are summarized by broad plant groupings (Table 2, p.55), but scientific names are not given, and most sources cited are also Finnish. Foot-loadings presented are those of Nasimovich (1955) and Kelsall (1969).

Chest height of Alces alces is noted as approximately 1 m "... and being a strong animal, it can manage even 2 m deep snow, while 50 cm appears to be the maximum of Capreolus capreolus and Odocoileus virginianus.

C. capreolus finds suitable winter habitats on steep slopes of river valleys and in the agricultural belts even in northern Finland, while O. virginianus inhabits the southwestern part of the country [where it was introduced], where maximum snow depth is 50 cm or less. Among the subspecies of Rangifer tarandus, the long-legged R. t. fennicus is the one best adapted to the deep snow cover of the taiga".

97 Ramaswamy, S.S., G.L. Dua, V.K. Raizada, G.P. Dimri, K.R. Viswantahan, J. Madhaviah, and T.N. Srivasttava. 1966. Effects of looseness of snow on energy expenditure in marching on snow-covered ground. J. App. Physl. 21: 1747-1749.

(Humans/Snow Depth/Energy//)

A quantitative study of the energy requirements of infantry soldiers while walking in snow of varying depths. Results were used to assess caloric requirements of soldiers on duty during snowy operational conditions. Oxygen requirements were found to increase linearly with depth of snow traversed until the imprints of the feet reached a depth of 37 cm. Oxygen requirements thereafter seemed to rise asymptotically.

98 Regelin, W.L. Nutritional interactions of black-tailed deer with their habitat in southeast Alaska. Pages 60-68 in O.C. Wallmo and J.W. Schoen (eds.). Sitka black-tailed deer: Proceedings of a conference in Juneau. USDA For. Serv. and Alaska Dept. of Fish and Game. Series No. R10-48.

(Sitka Deer/Snow Depth/Distribution, Food Availability/ U.S. West Coast)

During winter, Sitka deer in southeastern Alaska move into low elevation climax forest where shallow snow allows access to forage. Winter nutritional requirements are discussed. Logging can improve deer habitat (references given) but only in areas with low snowfall. Deer in southeast Alaska require old-growth timber; logging it is detrimental to deer populations.

99 Regelin, W.L., J.G. Nagy, and O.C. Wallmo. 1977. Effects of snowdrifts on mountain shrub communities. Proc. XIIIth Intl. Congress of Game Biologists, p.414-419.

(Mule Deer/Snow Depth, Snow Density/Food Availability/ U.S. Mountains)

Five snow fences were constructed on mule deer range in Middle Park, Colorado to determine the feasibility of

increasing availability of shrubs by relocating snowdrifts. Over 4 winters mean depth and mean density in protected stands was less than in controls ($P < 0.05$). Snow in protected shrub stands was not wind-deposited but remained in place after falling. "It was relatively easy for deer to travel through this light, fluffy snow, but they avoided the deep, hard, wind-packed snow in normal shrub stands". Shrub, forb, and graminoid density were not altered in the 4 years of study; neither was current annual growth measures of Amelanchier alnifolia or Symphoricarpus oreophilus. The discussion of deer use is anecdotal.

100 Robinson, W.L. 1960. Test of shelter requirements of penned white-tailed deer. J. Wildl. Manage. 24(4): 364-371.

(White-tailed Deer/Snow Depth/Energy/Eastern U.S.)

White-tailed deer were placed in three 1.5-acre enclosures each with different cover densities (34, 55 and 73% crown cover respectively). A below-maintenance diet was provided. Weather and animal conditions were monitored. Temperatures were lowest and snow depths and wind the highest in the cutover area. However, the deer formed trails and snow depth was, therefore, probably not a significant factor. There was no difference in deer condition between the three enclosures. This is attributable to deer's ability to find the most favourable microclimate.

101 Rongstad, O.J., and J.R. Tester. 1969. Movements and habitat use of white-tailed deer in Minnesota. J. Wildl. Manage. 366-379.

(White-tailed Deer/Snow Depth/Distribution/Eastern U.S.)

In the winter of 1963-1964, snow depths never exceeded 10 inches and deer home ranges remained between 400 and 600 acres. The time spent in cedar areas decreased from January to April. In 1964-1965, home ranges decreased from 342 acres in January to 186 acres in March as snow depth increased from 10 to 42 inches. The proportion of time spent in the cedars increased with increasing snow depth.

102 Russell, C.P. 1932. Seasonal migration of mule deer. Ecol. Monogr. 2: 1-46.

(Mule Deer/Snow Depth/Distribution/U.S. Mountains)

In years during which Yellowstone snow depths were 24-36 inches, deer and elk left the park for lower areas on the

Yellowstone River where they were shot or died of starvation.

103 Schneewis, J.C., K.E. Severson, L.F. Peterson, T.E. Schenck, R.L. Linden, and A.H. Richardson. 1972. Food habits of deer in the Black Hills. South Dakota Coop. Wildl. Res. Unit Bull. No. 606. 35 pp.

(White-tailed Deer/Snow Depth/Food Availability/ U.S. Mountains)

Litterfall consumption by white-tailed deer increased with increasing snow depth.

Not seen - cited in Jones 1975.

104 Segal, A.N. 1962a. Pasturing regime and periodicity of physiological functions in reindeer. Pages 130-150 in: Reindeer in the Karelian ASSR, Akad. Nauk, Petrozavodsk. (in Russian).

(Reindeer//Cratering, Energy/USSR)

Reindeer spend more than 5 hr day^{-1} cratering in Karelia.

Not seen - cited in Morrison (1964).

105 Segal, A.N. 1962b. Physiological characteristics of pasturing. Pages 151-165 in: Reindeer in the Karelian USSR, Akad. Nauk, Petrozavodsk. (in Russian).

(Reindeer//Cratering, Energy/USSR)

Metabolic measurements suggest caribou expend little more work cratering for food in winter than feeding in summer.

Not seen - cited in Morrison (1966), Fennia 86: 1-51.

106 Seton, E.T. 1909. Life-histories of northern animals; an account of the mammals of Manitoba. New York: Charles Scribner's Sons. 1267 pp.

(//Foot Loading/Boreal Canada)

Reported to have some very early determinations of foot loading. The abridged edition available in the UBC library has no mention of this.

107 Severinghaus, C.W. 1947. Relationship of weather to winter mortality and population levels among deer in the Adirondack region of New York. Trans. N. Am. Nat.

Resour. Conf. 12: 212-223.

(White-tailed Deer/Snow Depth, Snow Duration/Mortality/ Eastern U.S.)

White-tailed deer winter mortality was determined by strip-census between 1930-1946. Deaths mile-^{1} were compared with temperature and snowfall records. Snow depth and duration was the critical factor affecting winter mortality. Deep snow was more critical late in the season. Depths $\geq$ 20 inches were critical to deer because a fawn's chest height is 18-19 inches whereas an adult's is 20-22 inches. Sinking depth is the important factor and is influenced by crusts. Deer weaken rapidly when on a restricted range. In the area studied, deep snow must last 5 weeks to significantly affect deer mortality. When the duration exceeds 10 weeks, the effect becomes severe. Temperature is primarily a factor in that it retards snow loss.

108 Severinghaus, C.W. 1953. Springtime in New York - another angle. What goes on in our Adirondack deer yards. New York State Conservationist 7(5): 2-4.

(White-tailed Deer/Snow Depth, Climate/Food Availability, Distribution/Eastern U.S.)

Deer consistently choose sites which effectively moderate rigorous climate in preference to areas having plentiful browse.

Not seen - cited in Verme (1965).

Silver, R.S. 1976. Ecological features of moose (Alces alces andersoni) winter habitat in the boreal white and black spruce zone of northeastern British Columbia. M.Sc. thesis, Univ. of British Columbia, Vancouver. 278 pp.

(Moose/Snow Depth/Distribution/Boreal Canada)

A study of factors affecting winter dispersion of moose in an area northwest of Fort St. John, B.C. Snow depth was measured at 10 stations. Canopy cover was measured using a dot-grid overlay of photos taken with a fish-eye lens. Deciduous vegetation was ineffective at intercepting snow. Dense black spruce showed maximal accumulations - despite dense crown closure. Moose utilized coniferous forest only 20% of the time. Snow depth never reached the critical 76 cm depth and was not a critical factor.

109 Singer, F.L. 1979. Habitat partitioning and wildlife relationships of cervids in Glacier National Park. J. Wildl. Manage. 43: 437-444.

(Moose, Elk, White-tailed Deer/Snow Depth/Distribution/ U.S. Mountains)

Snow depth was the key factor determining habitat partitioning by moose, elk, and white-tailed deer. Open types had the most snow (mean = 80 cm) whereas Douglas-fir forests had the least (mean = 12 cm). Moose were more often found in open types whereas deer were more often in the dense Douglas-fir forest. All three species also utilized the spruce forest with intermediate snow depths (mean = 40 cm).

110 Skogland, T. 1978. Characteristics of the snow cover and its relationship to wild mountain reindeer (Rangifer tarandus tarandus L.) feeding strategies. Arctic and Alpine Res. 10(3): 569-580.

(Reindeer/Snow Hardness, Snow Depth/Distribution, Cratering/Europe)

Snow characteristics were related to the distribution and behaviour of feeding reindeer in Norway. Snow hardness was measured with a Ramsonnde and, in soft snow, spring gauges. In uncratered areas, Ramsonnde hardness increased from 40-140 kg from early to late winter as compared to 15-27 kg in cratered areas. In cratered areas, spring penetrometer hardness measurements increased from 200-400 g m^{-2} in early winter to 800-1000 g cm^{-2} in late winter. Pawing rates decreased linearly with increasing snow density and exponentially with hardness. Crater depths decreased with hardness and density. Since snow densities are usually adequate to support reindeer, the major influence of snow is to restrict the food supply.

111 Sobanski, G.G. 1975. Snow and migration of marals in the northeastern Altai. Soviet J. Ecology 6: 373-374.

(Elk/Snow Depth/Distribution, Movement/USSR)

The boundaries of winter range of the maral (Cervus elaphus sibiricus) "pulsate" with the amount of snow; the less snow, the greater the area. The earlier and greater the snowfall, the earlier is the move to winter range. Marals can "predict" snowfalls and move to winter range before the storm. These premonitions are not inherent in all individuals; many marals are caught by surprise on unsuitable range.

112 Spiker, C.J. 1933. Some late winter and spring observations on the white-tailed deer of the Adirondacks. Roosevelt Wildl. Bull. 6: 327-395.

(White-tailed Deer/Snow Depth/Distribution/Eastern U.S.)

A largely anecdotal account of deer wintering in the Adirondacks. In normal years, with snow depths of 3-4 feet, deer yard in spruce and balsam swamps. If the snow is not too deep, they forage in the surrounding hardwoods or second-growth.

113 Stardom, R.R.P. 1975. Woodland caribou and snow conditions in southeast Manitoba. Proc. 1st Int. Reindeer Caribou Symp.: 324-334.

(Caribou/Snow Depth, Snow Hardness/Distribution/Arctic-Subarctic)

A study of caribou movements in relation to snow conditions. Caribou fed on arboreal lichens in open bogs until snow depths approached 65 cm and crusts had hardness of 400 g cm^{-2} (NRC measurements). They then moved into jackpine-lichen rock ridges. Snow hardness had the greatest effect on caribou activity. In a year with above average snowfall, lakes were used frequently.

114 Sweeney, J. 1975. Elk movements and calving as related to snow cover. Ph.D. thesis, Colorado State Univ., Fort Collins, CO. 95 pp.

(Elk/Snow Depth, Snow Hardness, Distribution/Movement, Cratering/U.S. Mountains)

Snow depths of 40 cm did not impair the mobility of elk whereas greater depths produced movements to areas with less snow. Elk can paw through only about 40 cm of snow. Physical limitations in movement (critical depth) occur at about 70 cm. Discusses interactions between depth and hardness.

115 Telfer, E.S. 1967. Comparison of moose and deer winter range in Nova Scotia. J. Wildl. Manage. 31(3): 418-425.

(White-tailed Deer, Moose/Snow Depth/Distribution, Movement/Eastern Canada)

In Nova Scotia, deer retreated from the highlands in winter whereas moose did not. Mean winter snow depths and densities showed no differences between deer and moose areas, although April snow depths were much greater in the moose area. The moose area had 30 inches of snow - an amount thought unlikely to hinder moose. In the spring, deer moved to deep snow areas to feed early on cold mornings but returned before the sun softened the crust. The lack of association between deer and moose in winter may hinder the transmission of Pneumostrongylus tenuis ("moose sickness").

116 Telfer, E.S. 1970. Winter habitat selection by moose and white-tailed deer. J. Wildl. Manage. 34: 553-559.

(Moose, White-tailed Deer/Snow Depth/Distribution, Sinking Depth/Eastern Canada)

A total of 58 twenty-chain transects in New Brunswick were classified as to forest type and stand density. At points where deer or moose tracks crossed the transect, snow depth, track depth, and forest type were recorded. Data were collected in January and March. In January, deer utilized dense coniferous and mixed wood stands where snow depths averaged 29 cm vs 39 cm for all stand types. Moose used dense stands less than would be expected if their use were random. In March, both deer and moose used dense coniferous stands more than expected. There was no difference in the sinking depths of moose and deer. Moose and deer used 69% of the area in January and 22% in March. The proportion of overlap was 9% in January and 1% in March.

117 Telfer, E.S., and J.P. Kelsall. 1971. Morphological parameters for mammal locomotion in snow. Presented at 51st Ann. Meet. American Society of Mammalogists. Univ. of British Columbia, 20-24 June.

(Bison, Elk, Moose, White-tailed Deer//Sinking Depth/ Canadian Mountains)

Measurements of chest heights, foot area, weight, and foot-loading of bison, elk, moose, and white-tailed deer in Elk Island National Park. Replicable measuring procedures are described. Chest heights of the three cervids differed by a fixed interval suggesting resource partitioning with respect to snow. Sex and age differences in morphology may relate to winter mortality.

118 Telfer, E.S., and J.P. Kelsall. 1979. Studies of morphological parameters affecting ungulate locomotion in snow. Can. J. Zool. 57: 2153-2159.

(Deer, Moose, Elk, Bison//Foot Loading/Canadian Mountains)

Body weight, chest height, and various hoof measurements were made on moose, wapiti, white-tailed deer, and bison carcasses obtained in slaughter reductions in Elk Island and Jasper National Parks, Alberta. The separation in chest heights of fully mature deer, wapiti, and moose suggests a morphological adaptation to resource partitioning based on differential ability to exploit various snow depths. White-tailed deer exhibit the smallest foot-loading; male bison the greatest. There are significant sex differences between sexes and ages in both chest height and foot-loading.

119 Teplova, E.N., and V.P. Teplov. 1947. Importance of the snow cover in the ecology of mammals and birds in the Pechero-Il'ych State Park. Tr. Pecher-Ilychsk. Goszarovednika No. 5. (in Russian).

(Other Species//Sinking Depth/USSR)

Loading weight was determined by dividing the animal's weight by the surface area of all its feet. Foot loadings of 12 g cm^{-2} and 28 g cm^{-2} were determined for "white hares" and otters respectively.

Not seen - cited in Burdukov and Kozlov (1979).

120 Thing, H. 1977. Behavior, mechanics, and energetics associated with winter cratering by caribou in northwestern Alaska. Biological papers of the Univ. of Alaska 18. 41 pp.

(Caribou/Snow Depth, Snow Hardness/Cratering, Movement/ Arctic-Subarctic)

Caribou usually crater with their right front foot. Percentage of active time spent cratering is 15%, 17% and 18% for calves, yearlings and adults respectively. Calves often use their mothers' craters. Weights and lengths for segments of the appendicular skeleton are provided. Weight-load-on-hoof is discussed in terms of number of feet touching the snow simultaneously during movement. It is suggested that loadings are 500 g cm^{-2} for walking and 1000 g cm^{-2} for galloping. Snow hardness in cratered areas was 714 g cm^{-2} (NRC measurements) in October-November and 2311 g cm^{-2} in March-April. Mean density also increased. Crater volume decreases in late winter. Caribou leave a feeding area when 1/3 of the area is disturbed. Detailed analysis of mechanics and energetics of cratering, based on film records, is provided.

121 Tushinskii, G.K. 1949. Laving, vozniknovenie i zashchita ot nikh. (Occurrence of avalanches and protection against them). Moscow: Geographical Literature.

(Reindeer/Snow Depth/Distribution, Food Availability/ USSR)

Crater site selection in reindeer is olfactory. Convective air currents in the snowpack permit the animals to smell forage. The odour is strongest where the snow is shallowest. This explains why reindeer select the shallowest snow for cratering.

Not seen - cited in LaPierre and Lent (1977).

122 Van Camp, J. 1975. Snow conditions and the winter feeding behaviour of Bison bison in Elk Island National Park. Can. Wildl. Serv. Rpt., Edmonton.

(Keywords to come)

not seen.

123 Verme, L.J. 1965. Swamp conifer deer yards in northern Michigan. J. Forestry 63: 523-529.

(White-tailed Deer/Snow Depth/Distribution, Food Availability/Eastern U.S.)

A study of winter range use by white-tailed deer in Michigan conifer swamps. All-age forests were unused, despite an abundance of food, because cover was lacking. Cutting programs which resulted in a mosaic of cover types resulted in overuse of white cedar and population eruptions and crashes. Silvicultural practices should attempt to create large blocks of even-aged stands with a differential between blocks of 15-20 years and a rotation of 80-100 years. Clearcutting in long strips is advocated. Each cutting must be large enough to exclude deer from the clearing while reproduction is being established.

124 Verme, L.J. 1968. An index of winter weather severity for northern deer. J. Wildl. Manage. 32: 566-574.

(White-tailed Deer/Snow Depth, Snow Hardness/Sinking Depth, Mortality/Eastern U.S.)

Includes plans for the construction of a "chillometer" - a self-integrating recorder of atmospheric chill. Describes the "compaction gauge" - a two foot, 3 lb, lead-filled piece of copper pipe which is dropped from the surface of the snow. Temperature and wind were the major factors affecting chillometer heat loss whereas solar radiation, snowfall, and relative humidity were relatively minor agents. The compaction gauge was found to closely reflect sinking depth except in areas with weak surface crusts. A winter severity index is described as the sum of weekly air chill and snow hazard. The index seems to be related to winter mortality.

125 Verme, L.J., and J.J. Ozoga. 1971. Influence of winter weather on white-tailed deer in upper Michigan. Pages 16-28 in: A.O. Haugen (ed.), Proc. Snow and Ice in Relation to Wildlife and Recreation Symposium. Iowa St. Univ., Ames, Iowa.

(White-tailed Deer/Snow Depth, Snow Hardness/Mortality/

Eastern U.S.)

A study of winter weather (1964-1966) on deer activity and mortality in Michigan. "Snow hazard" was determined by depth plus a support factor determined from a compaction gauge. A "chillometer" (Verme 1968) determines atmospheric chill. Snow conditions were determined not to be particularly hazardous to deer during mid-winter. Cold is of equal or greater importance.

126 Wallmo, O.C., and R.B. Gill. 1971. Snow, winter distribution, and population dynamics of mule deer in central Rocky Mountains. Pages 1-15 in: Proc. Snow and Ice in Relation to Wildlife and Recreation Symposium. Iowa St. Univ., Ames, Iowa.

(Mule Deer/Snow Depth/Distribution, Mortality/ U.S. Mountains)

Tame deer seemed undeterred by 10 inches of powder snow, but would not wander or graze freely in 16 inches of uncrusted snow. Twelve inches seemed a threshold depth. Data are given comprising > 10,000 observations showing that deer seek both general areas and local areas with less snow. Correlations of -0.87 were found between winter snowfall and deer counts in the subsequent year indicating a tight linkage with winter mortality. In 3 of 4 years, winter precipitation was reflected in yearling does killed in the next year, indicating a winter nutrition effect on productivity.

127 Ward, A.L., K.L. Diem, and R.W. Weeks. 1975. The impact of snow on elk. Pages 165-174 in: P.H. Knight et al. (eds), The Medicine Bow Ecology Project, Univ. Wyo., Laramie.

(Keywords to come)

Not seen.

128 Webb, W.N. 1948. Environmental analysis of a winter deer range. Trans. N. Am. Wildl. Conf. 13: 442-450.

(White-tailed Deer/Snow Depth, Slope/Food Availability/ Eastern U.S.)

Winter range in the Adirondacks was map-grided into 40 acre blocks. Deer avoided north slopes and preferred the steepest slopes and level ground. The hardwood type was avoided while spruce flats and swamps were heavily utilized. The biotic and topographic factors interacted. Occurrence and density of plant species yielded cover and food "ratings". The average food rating on concentration

areas was 77 vs an average rating of 91 for all areas. The average cover rating in concentration areas was 69, vs 60 on areas not used in concentration. These observations support the theory that concentrations occur in the densest forest where lack of food is common. Level areas produced the least food and most cover; the opposite applies for north slopes.

The discussion following this article contains interesting questions and speculations concerning manipulation of forest types to improve winter range.

129 Weger, E. 1977. Evaluation of winter deer use of second growth stands by black-tailed deer. B.S. thesis, Univ. of British Columbia, Vancouver. 42 pp.

(Black-Tailed Deer/Snow Depth/Distribution/Canadian West Coast)

A study of black-tailed deer winter habitat use in the Nanaimo River watershed during a particularly mild winter. Pellet counts showed mature timber was used more heavily than immature stands. Snow depths increased with elevation and were deeper in immature stands. Higher track counts were recorded at lower elevations and in mature timber.